

Identification and distribution of cotton rats, genus *Sigmodon* (Muridae: Sigmodontinae), of Nayarit, México

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Abstract.—Morphological, chromosomal, distributional, and ecological data are presented for three species of *Sigmodon* (*S. alleni*, *S. arizonae*, and *S. mascotensis*) from the state of Nayarit, México. The species were collected in all possible pairwise combinations of sympatry, including the first record of such documented for *S. arizonae* and *S. mascotensis*. Emphasis is devoted to the discrimination of *S. arizonae* and *S. mascotensis*, from each other and from typical *S. hispidus*, using qualitative features of the skin and skull and morphometric analyses of craniodental measurements. Based on these results and examination of type specimens, additional synonyms of *S. mascotensis* are identified, with reassignment of two forms, *tonalensis* Bailey (1902) and *obvelatus* Russell (1952), currently mistaken as subspecies of *S. hispidus*. *Sigmodon mascotensis* emerges as a species distributed from southern Nayarit and Zacatecas to extreme western Chiapas, where it inhabits deciduous or semi-deciduous tropical vegetation having a pronounced dry season. These reallocations and other reidentifications remove any documentation for *S. hispidus* along the entire Pacific versant of México.

A useful form of research communication that sees less application today is the brief expeditionary account or short faunal note. Aside from the practical enhancements in knowledge of a taxon's distribution and habitat, such reports offer the advantage of bringing regionally focussed nomenclatural clarity to complex taxonomic problems that seem incomprehensible over a broader geographic scale. One recalls that the prolific literature appearing over the past two decades on the *Peromyscus boylii* group emanated from Hooper's (1955) memorable commentary in "Notes on Mammals of Western México," in which he recorded the sympatric occurrence of various "morphological types" of *boylii* at several collecting localities in Jalisco, Nayarit, and Sinaloa (see systematic reviews by Carleton 1989, and Bradley et al. 1996).

The regional focus here is Nayarit, Mé-

xico, and the taxon of interest is the genus *Sigmodon*, the ecologically abundant cotton rats that inhabit open landscapes from the southern United States, through México and Middle America, to northern South America (Hall 1981, Voss 1992). Situated along coastal westcentral México, the state of Nayarit encloses a varied topography and diverse natural environments, a biogeographical setting that has proven pivotal for illuminating the systematics of other small mammals (for example, Fisher & Bogan 1977, Gardner 1977, Bogan 1978, Diersing & Wilson 1980, Carleton et al. 1982, Wilson 1991).

The excellent series of Nayarit cotton rats collected by personnel of the U.S. Fish and Wildlife Service in the middle 1970s warrant report in view of Zimmerman's (1970) seminal report on *Sigmodon* taxonomy. His study, and the subsequent contributions of

Severinghaus & Hoffmeister (1978) and Hoffmeister (1986), revealed the greater species diversity and distributional complexity of *Sigmodon* found in the southwestern United States and northwestern México. In this report, we document the kinds and distribution of *Sigmodon* species in Nayarit (*S. alleni*, *S. arizonae*, and *S. mascotensis*); review morphological and chromosomal characteristics for identifying the species, with emphasis on discrimination of *S. arizonae* and *S. mascotensis*; and amplify the known geographic range of *S. mascotensis* in western México, including the reallocation of forms currently classified as subspecies of *S. hispidus* (namely, *Sigmodon hispidus tonalensis* Bailey, 1902, and *Sigmodon hispidus obvelatus* Russell, 1952).

Materials and Methods

The 214 specimens of Nayarit *Sigmodon* that form the nucleus of this report are contained in the National Museum of Natural

History, Smithsonian Institution, Washington, D.C. (USNM, the abbreviation for the former United States National Museum). A few originated from the pioneering Biological Survey of México conducted by E. A. Goldman and E. W. Nelson (1897 expedition to Tepic; see Goldman 1951), but most were collected recently (1975–1977) by personnel associated with the U.S. Fish and Wildlife Service (now part of the USGS Patuxent Wildlife Research Center), pursuant to a faunal analysis of Nayarit mammals. Other specimens reported here, including holotypes and type series, are housed in the American Museum of Natural History, New York (AMNH); the Field Museum of Natural History, Chicago (FMNH); Museum of Natural History, University of Kansas, Lawrence (KU); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); The Museum, Michigan State University, East Lansing (MSU); and Texas Cooperative Wildlife Collections, College Station (TCWC).

Table 1.—Gazetteer of collecting localities (see Fig. 1).

Locality	Elevation (meters)	Coordinates N/W
1. Tacote, 1.4 mi N	15	22°38'/105°27'
2. Río Canas, near La Concha	20	21°31'/105°26'
3. Acaponeta	46–75	22°29'/105°21'
4. Cuautla, 1 mi S	0	22°12'/105°38'
5. Santa Cruz, 6 km S	0	21°56'/105°35'
6. Playa Colorado	0	21°53'/105°34'
7. Playa Los Corchos, 4 mi E	0	21°43'/105°25'
8. San Blas	0	21°32'/105°17'
9. Aticama, 4 km S	50	21°27'/105°11'
10. Chacala	30	21°10'/105°13'
11. Lo de Marcos, 1 mi S	0	20°57'/105°21'
12. El Venado, 3.5 mi E	100	22°57'/104°57'
13. Arroyo de Jiguite	100	21°49'/104°48'
14. El Casco, 1.2 mi S	60	21°45'/104°51'
15. La Villita, 1 km S	760	21°35'/104°56'
16. Tepic	1000	21°30'/104°53'
17. San Pedro Lagunillas, 2 mi E	1300	21°12'/104°43'
18. Estanzuela	1380	21°16'/104°28'
19. Coapan, 1.8 mi NW	1560	21°09'/104°29'
20. Ahuacatlán, 8 mi S	1500	20°58'/104°28'
21. Mesa del Nayar	1300	22°12'/104°39'
22. Ocota Airstrip	1900	21°50'/104°13'
23. Rancho Sapotito	1100	21°20'/103°58'

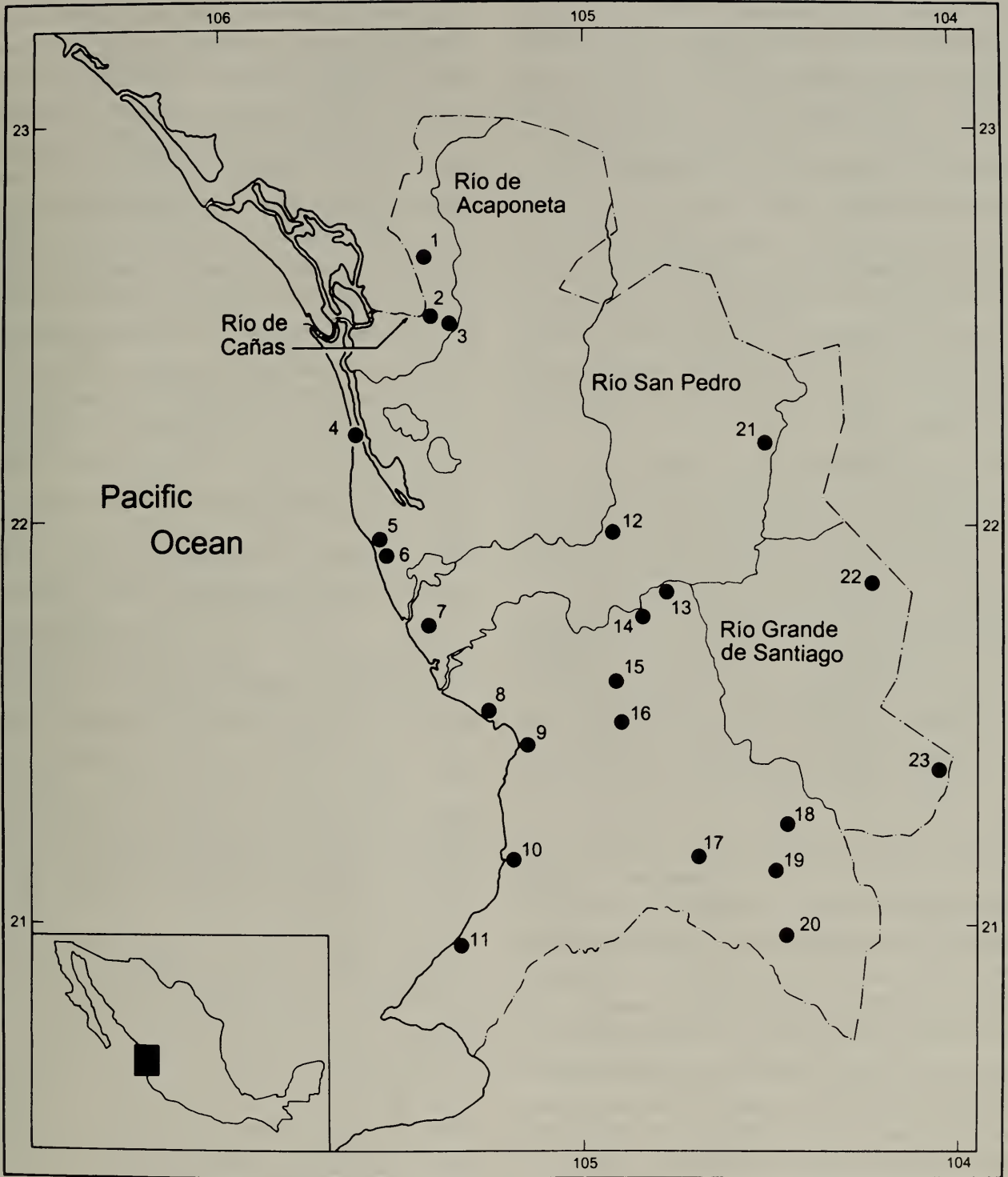


Fig. 1. State of Nayarit, México, illustrating collecting localities of *Sigmodon* specimens housed in the National Museum of Natural History (numbers refer to sites listed in Table 1).

Twenty-three Nayarit localities are represented in the preserved material (Table 1, Fig. 1). Coordinates of collecting sites were later determined from 1:50,000 topographic maps used by the field teams and annotated with the localities visited; most elevations were recorded in the field with an altimeter

and later verified against the same topographic series.

Animals were generally preserved as conventional study skins and skulls but also as complete skeletons and formalin-fixed, whole carcasses stored in alcohol. Preparation of standard chromosomal spreads,

definition of fundamental number (FN), and descriptive terminology for chromosomal morphology follow Patton (1967) and Gardner & Patton (1976). The 32 voucher specimens for the karyotypic variation reported are contained in USNM and represent the localities listed next.

Sigmodon alleni: Nayarit, Arroyo de Jiguite, Río Santiago, 1 ♂ (523935); 4 km S Aticama, 1 ♂ (524480), 2 ♀ (524478, 524479); Chacala, 1 ♀ (523934); 1.2 mi S El Casco, 1 ♀ (511699); 1 mi S Lo de Marcos, 1 ♂ (523943), 3 ♀ (523940–523942).

S. arizonae: Nayarit, Mesa del Nayar, 1 ♀ (511700); Ocotá Airstrip, 2 ♂ (523948, 523950), 4 ♀ (523946, 523947, 523949, 523951). Sinaloa, Microondas La Muralla, 1 ♂ (524487), 1 ♀ (524486).

S. mascotensis: Nayarit, 8 mi S Ahuacatlán 1 ♂ (523953), 2 ♀ (523952, 523954); Arroyo de Jiguite, Río Santiago, 4 ♂ (523962, 523963, 523965, 523966), 1 ♀ (523964); Rancho Sapotito, 2 ♂ (511703, 511704), 3 ♀ (511702, 511705, 511706).

We recorded 5 external, 18 cranial, and 3 dental dimensions (in millimeters, mm) to summarize patterns of variation within and between the populations sampled. Total length, length of tail vertebrae, hindfoot length, length of pinna from notch, and mass (weight in grams, g) were transcribed from skin labels. Crania were viewed under a dissecting microscope when measuring the 21 craniodental variables to 0.01 mm with hand-held, digital calipers accurate to 0.03 mm. These measurements, their abbreviations as used in tables and figures, and their landmark definitions where clarification is necessary, include (see Carleton and Musser, 1995, for illustration of most anatomical endpoints): occipitonasal length (ONL); zygomatic breadth (ZB); least interorbital breadth (IOB); breadth of braincase (BBC)—taken behind the squamosal root of the zygomatic arches, the caliper's jaws resting on the squamosal bones just above the flange (inferior temporal ridge)

extending from the arches; breadth across occipital condyles (BOC); depth of braincase (DBC); distance between temporal ridges (DTR)—vertical distance between the dorsal margin of the superior temporal ridge and the ventral edge of the inferior temporal ridge (see Fig. 8); length of rostrum (LR)—measured oblique to the mid-longitudinal cranial axis, from the innermost bevel of the right zygomatic notch to the end of the nasals at their midsagittal junction; breadth of rostrum (BR)—distance across the lateralmost convexity of the nasolacrimal capsules; postpalatal length (PPL); length of bony palate (LBP); breadth of bony palate (BBP); length of incisive foramen (LIF); length of diastema (LD); breadth of zygomatic plate (BZP); length of zygomatic spine (LZS)—distance between the anterior orbital rim and the tip of the zygomatic spine; length of auditory bulla (LAB); coronal length of maxillary toothrow (LM1-3); coronal width of upper first molar (WM1); depth of upper incisor (DI); depth of mandible (DM)—distance, taken on the lateral surface of the dentary, from the rim of the m1 alveolus to the ventralmost projection of the mental symphysis.

Relative age was coarsely indexed by degree of molar wear according to the four age-classes recognized by Carleton and Musser (1989)—juvenile (J), young (Y), full (A), and old-adult (O). The distinction between juvenile and young adult cohorts based on upper third molar eruption constituted a more objective criterion of age recognition than did the assignment of individuals among the three adult classes based on gradations of wear. Among specimens with annotation of their reproductive state, many we assigned as young or full adult based on tooth wear exhibited signs of reproductive maturity (testis scrotal, evidence of lactation, counts of embryos or embryo scars), whereas those classified as juveniles did not.

To augment sample sizes for the various morphometric comparisons, Nayarit speci-

mens were grouped into eight analytical samples (operational taxonomic units, OTUs), as defined below (locality numbers correspond to those identified in Table 1 and Fig. 1). To provide a comparative standard, we included a homogeneous series of *Sigmodon hispidus*, sensu stricto, as a ninth OTU (U.S.A., Florida, Wakulla Co., St. Marks National Wildlife Refuge; $n = 53$; USNM 526059–526106, 527358, 527359, 527362–527364). Since most collectors at this locality also participated in the Nayarit survey, one can expect procedural conformity in the measurement of external variables.

Sigmodon alleni: OTU 1, $n = 20$, localities 8–15.

S. arizonae: OTU 2, $n = 9$, localities 2–7; OTU 3, $n = 25$, locality 17; OTU 4, $n = 6$, locality 22.

S. mascotensis: OTU 5, $n = 27$, locality 13; OTU 6, $n = 46$, locality 17; OTU 7, $n = 12$, localities 18–20; OTU 8, $n = 6$, locality 23.

S. hispidus: OTU 9, $n = 53$, Florida.

Standard descriptive statistics (mean, range, standard deviation) were obtained for the OTUs. Principal components and canonical variates were extracted from the variance-covariance matrix and computed using natural logarithmic transformations of the 21 craniodental variables. Loadings are expressed as Pearson product-moment correlation coefficients of the principal components or canonical variates with the original skeletal and dental variables. All univariate and multivariate computations were generated using Systat (Version 7.0, 1997), a series of statistical routines programmed for microcomputers.

Discrimination of Nayarit *Sigmodon* and Comparisons with *Sigmodon hispidus*

Intrasample age and sex variation.—Field and lab workers who study *Sigmodon* populations have regularly commented on the considerable ontogenetic variation encountered (e.g., Chipman 1965, Baker

1969, Voss 1992, Zelditch et al. 1992). Cotton rats are highly precocial and weaned animals soon enter the trappable population; seasonal differences in age composition of a population, as well as differences in growth rates between age cohorts, may be remarkable (Layne 1974, Slade et al. 1984). In view of such demographic factors, we found age variation to be equally conspicuous in all species samples of *Sigmodon* reported here, an impression quickly formed from superficial observation of crania and their wide range in size, shape, and rugosity. Casual visual impressions are reinforced by statistical comparisons among age groups in the large sample of *S. hispidus* (Table 2). Nearly all measurements display regular, incremental increases in size across the four age classes we defined, producing age-correlated differences that contribute substantially to nongeographic variation within our locality samples. Notable exceptions include dimensions of the molars (LM1-3, WM1), which once erupted decrease in crown height with occlusal use but do not grow in size; in contrast, girth of the incisor (DI) enlarges appreciably as cotton rats age.

The contribution of sexual dimorphism to intrasample variation, on the other hand, is hardly apparent, at least given the unbalanced nature of analyzable material usually consolidated from museum collections. Only two (IOB, DTR) of the 21 craniodental measurements yielded significant differences according to sex (Table 2), and these are sufficiently infrequent and incidental to suggest sampling error as an explanation.

Other than procedural elimination of the youngest age class, juveniles, we did not adjust for size in the morphometric analyses. Although variation attributable to post-weaning growth may be substantial within samples of *Sigmodon*, it is typically negligible relative to the interspecific contrasts that proved to be taxonomically important. In this respect, patterns of morphometric differentiation among cotton rats, their con-

Table 2.—Arithmetic means of craniodental variables and results of one-way ANOVAs for sex and age cohorts in a large sample of *Sigmodon hispidus* from Florida (OTU 9, $n = 53$).

Variable	Sex		f (sex)	Age				f (age)
	M (31)	F (22)		J (3)	Y (13)	A (29)	O (8)	
ONL	34.8	34.3	1.0	30.2	32.8	34.9	37.0	33.1***
ZB	19.5	19.3	1.5	17.2	18.7	19.5	20.3	21.7***
IOB	5.2	5.1	4.2*	4.8	5.0	5.2	5.3	7.8***
BBC	14.4	14.2	2.1	13.5	14.2	14.4	14.7	8.3***
BOC	7.5	7.5	0.4	7.5	7.4	7.4	7.7	1.9
DBC	10.7	10.7	0.5	10.1	10.6	10.7	11.2	8.6***
DTR	3.1	2.9	7.2**	2.4	3.0	3.1	3.3	12.4***
LR	11.6	11.5	0.2	9.8	10.9	11.7	12.5	21.4***
BR	6.7	6.6	0.9	6.1	6.3	6.7	7.3	22.8***
PPL	12.2	12.0	0.4	10.5	11.3	12.2	13.3	34.1***
LBP	6.6	6.5	1.7	6.1	6.3	6.7	6.7	6.2**
BBP	7.7	7.7	0.2	7.0	7.5	7.8	8.1	24.1***
LIF	7.8	7.7	0.1	6.7	7.3	7.9	8.5	19.8***
LD	9.6	9.3	1.1	8.1	8.7	9.7	10.5	31.5***
BZP	3.9	3.7	2.8	3.2	3.7	3.9	4.1	9.7***
LZS	4.6	4.4	1.3	3.6	4.3	4.6	4.9	11.3***
LAB	6.3	6.3	0.0	6.1	6.1	6.4	6.5	6.3**
LM1-3	6.4	6.4	0.2	6.4	6.4	6.4	6.3	0.5
WM1	2.1	2.1	0.5	2.1	2.1	2.1	2.1	0.5
DI	2.0	2.0	0.4	1.6	1.9	2.0	2.1	49.0***
DM	6.4	6.3	1.6	5.6	6.1	6.5	6.6	14.9***

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

spicuous age variety notwithstanding, are much like those derived for other closely related, congeneric species of New World muroids (e.g., Carleton & Musser 1989, 1995; Voss & Marcus 1992, Hofer et al. 1999).

Morphometric variation.—Covariation patterns derived from the 21 original craniodental variables suggest two kinds of large *Sigmodon* among Nayarit populations (Fig. 2). These clusters correspond to the species *S. arizonae* and *S. mascotensis* (Figs. 3, 4), identifications independently corroborated by agreement of karyotyped specimens with currently understood differences in diploid number ($2N = 22$ or 28 ; Zimmerman 1970) and by contrasts in certain qualitative features (see below). The “correct” phenetic association of relevant holotypes—*arizonae*, *major*, and *mascotensis* (Fig. 2)—bolsters the use of these names for the Nayarit populations. Greater size in all dimensions accounts for separation of *S.*

mascotensis and *S. arizonae* on the first principal component (loadings uniformly large and positive—Table 3); the generous proportions of the latter’s molars provide most discrimination on the second component (LM1-3 and WM1 correlations relatively large and negative). The resulting constellations of specimen scores conform to the now familiar ordination pattern evidenced between morphologically similar, closely related (congeneric) species of Muroidae; furthermore, their elongate spread and orientation, oblique to the bivariate plot of PC I and PC II, suggest the interplay of consistent interspecific shape differences and age-related size increases (Voss et al. 1990, 1992). Included among our samples is one locality where the two species were collected in sympatry (2 mi E San Pedro Lagunillas).

Unambiguous specific discrimination is preserved in the discriminant function analysis of the eight OTUs representing *S. ar-*

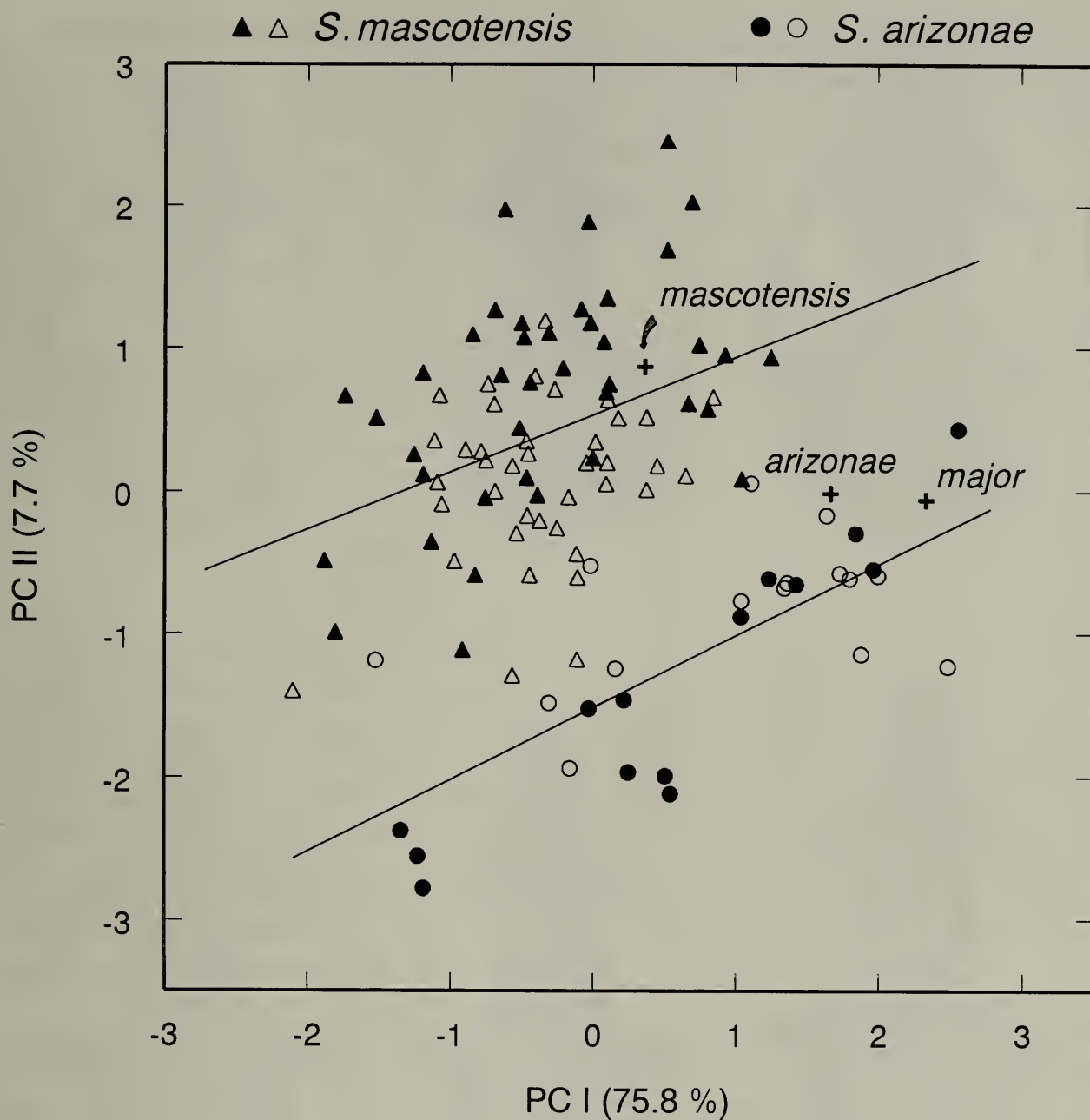


Fig. 2. Plot of first and second principal components extracted from analysis of 21 log-transformed craniodental variables measured on intact specimens of Nayarit *Sigmodon arizonae* ($n = 29$) and *S. mascotensis* ($n = 79$). Open symbols indicate specimens collected in close proximity at 2 mi E San Pedro Lagunillas, 1300 m; crosses refer to relevant type specimens discussed in the text. Regression lines of PC II on PC I differ significantly between species in their y-intercepts (0.54 versus -1.50 ; $F = 144.9$, $P < 0.001$) but not their slopes (0.42 versus 0.51; $F = 0.3$, $P = 0.553$). See Table 3.

arizonae, *S. mascotensis*, and *S. hispidus* (Fig. 5). Separation of Floridian *S. hispidus* on the first canonical variate extracted primarily results from differences in three variables (Table 4)—the larger size of the auditory bullae (LAB), the narrower distance between the temporal ridges (DTR), and, perhaps in correlation with the latter, the shallower braincase (DBC). LAB also generated the largest f -value in one-way anal-

yses of variance of the 21 craniodental measurements among the three species. Less conspicuously, the relatively greater length of the facial region in *S. hispidus* is reflected in the moderate, positive loadings for lengths of rostrum and incisive foramen, whose univariate means match those of the bigger *S. arizonae*. The generally larger values and comparable range (mostly -0.5 to -0.7) of correlations on the second ca-

Table 3.—Results of principal component analysis and one-way ANOVAs performed on all intact specimens of *Sigmodon arizonae* ($n = 29$) and *S. mascotensis* ($n = 79$) from Nayarit, México (see Fig. 2).

Variable	Correlations		ANOVAs f (species)
	PC I	PC II	
ONL	0.97	0.15	20.9***
ZB	0.98	0.02	55.1***
IOB	0.75	0.07	4.1*
BBC	0.88	-0.20	70.0***
BOC	0.78	-0.22	32.1***
DBC	0.81	0.08	21.0***
DTR	0.82	-0.01	50.0***
LR	0.94	0.16	19.4***
BR	0.95	0.16	17.8***
PPL	0.96	0.13	23.9***
LBP	0.78	0.13	8.1**
BBP	0.94	-0.13	41.9***
LIF	0.94	0.01	44.3***
LD	0.96	0.18	22.9***
BZP	0.86	0.28	2.7
LZS	0.88	0.16	12.9***
LAB	0.85	-0.33	144.5***
LM1-3	0.64	-0.70	189.3***
WM1	0.53	-0.79	206.6***
DI	0.92	0.15	11.1**
DM	0.97	0.10	28.2***
Eigenvalue	15.9	1.6	
% Variance	75.8	7.7	

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

nonical variate are more suggestive of general size and again underscore the robust proportions of *S. arizonae* apparent in visual inspection of skulls; the substantial dimensions of its molars (LM1-3, WM1) are particularly noteworthy in this regard. Samples of *S. mascotensis* approximate that of *S. hispidus* on the second axis.

A posteriori classifications of type specimens historically associated with the *S. hispidus* complex, as implemented in discriminant function analysis of the same eight OTUs, accord with some present taxonomic alignments and dispute others. The nomenclatural significance of these statistical assignments is considered in the Discussion and Taxonomic Summary (Fig. 17, Table 6—see below).

Sorting examples of Nayarit *S. alleni* from those of *S. arizonae* and *S. mascoten-*

sis is straightforward based on pelage color (see below) or diploid number ($2N = 52$; Zimmerman 1970). Yet in cranial size and discrete characteristics, *S. alleni* (Fig. 6) unexpectedly proved somewhat difficult to distinguish from *S. mascotensis*; for example, most univariate measurements of the two overlap extensively (Appendix) and disclose relatively few significant differences between means (Table 5). Principal component analysis of log-transformed variables nonetheless supplied clear separation of the two species based on crania alone (Fig. 7). The variables most influencing discrimination represent measurements taken on the braincase (DBC, DTR), zygoma (LZS), and molars (LM1-3, WM1), each of which is notably greater in *S. mascotensis* (Table 5; Appendix). Holotypes of interest within the region appropriately associate with their respective Nayarit populations, those of *mascotensis* and *colimae* more so and that of *alleni* less so. Although the disposition of the type specimen of *alleni* was somewhat peripheral as divulged in PCA, discriminant function analysis based on all nine OTUs (not illustrated) indisputably placed the holotype with the Nayarit sample of the taxon.

Although external dimensions were excluded from multivariate examination, they generally reflect the same pattern of interspecific size contrasts noted for craniodental variables and supply helpful guidance for first-approximation field or museum identification (Appendix). The absolutely short and relatively narrow hind foot of *S. alleni*, for example, readily separates that species from young examples of *S. mascotensis*. As noted by Bailey (1902), hindfoot size and tail length, absolute and relative, help to distinguish *S. mascotensis* from examples of *S. h. hispidus* and *h. berlandieri*. Relative length of tail in *S. mascotensis* (TL ca. 45% of TOTL) also exceeds that in the larger-bodied *S. arizonae* (TL ca. 40% of TOTL), a species which otherwise stands apart for its exceptional mass and size in all other external variables quantified.

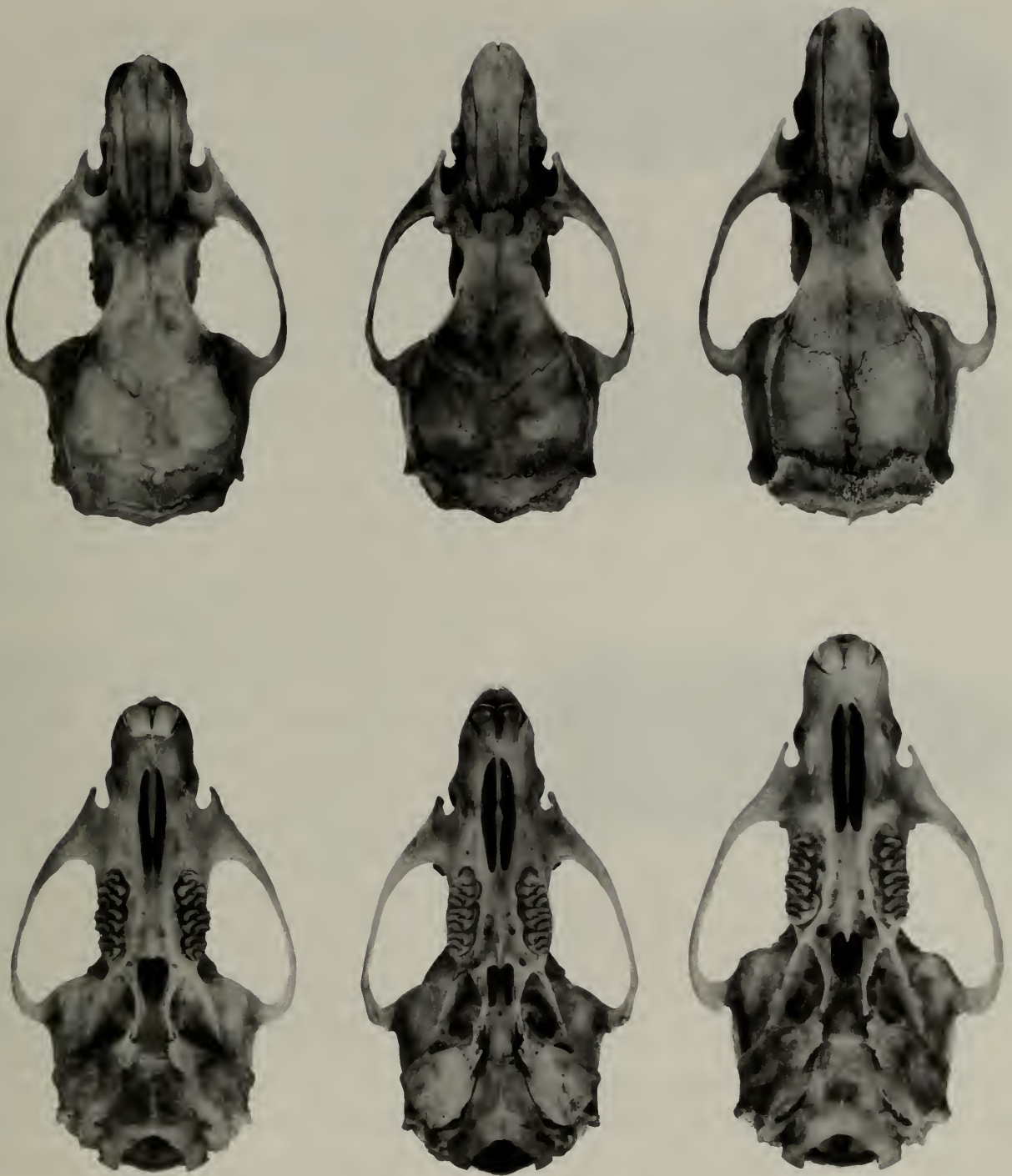


Fig. 3. Dorsal and ventral cranial views (about 1.75 \times) of adult *Sigmodon*: left pair, *S. mascotensis* (USNM 510026), a male from 2 mi E San Pedro Lagunillas, Nayarit; middle pair, *S. hispidus berlandieri* (USNM 157382), a male from 8 mi E Deming, New México; and right pair, *S. arizonae* (USNM 510040), a female from 2 mi E San Pedro Lagunillas, Nayarit.

Qualitative cranial traits.—Zimmerman (1970) identified several consistent cranial differences among *Sigmodon* populations that corresponded to the chromosomal contrasts he documented and to the three species he recognized among his samples—namely, *S. hispidus*, *S. arizonae*, and *S. mascotensis*. Other useful qualitative traits

were advanced by Severinghaus & Hoffmeister (1978) and Hoffmeister (1986), particularly for separation of *S. hispidus* from *S. arizonae* in the southwestern United States. We here extend the utility of select cranial features to the Nayarit populations formerly included under *S. hispidus*.

The vertical distance between the supe-

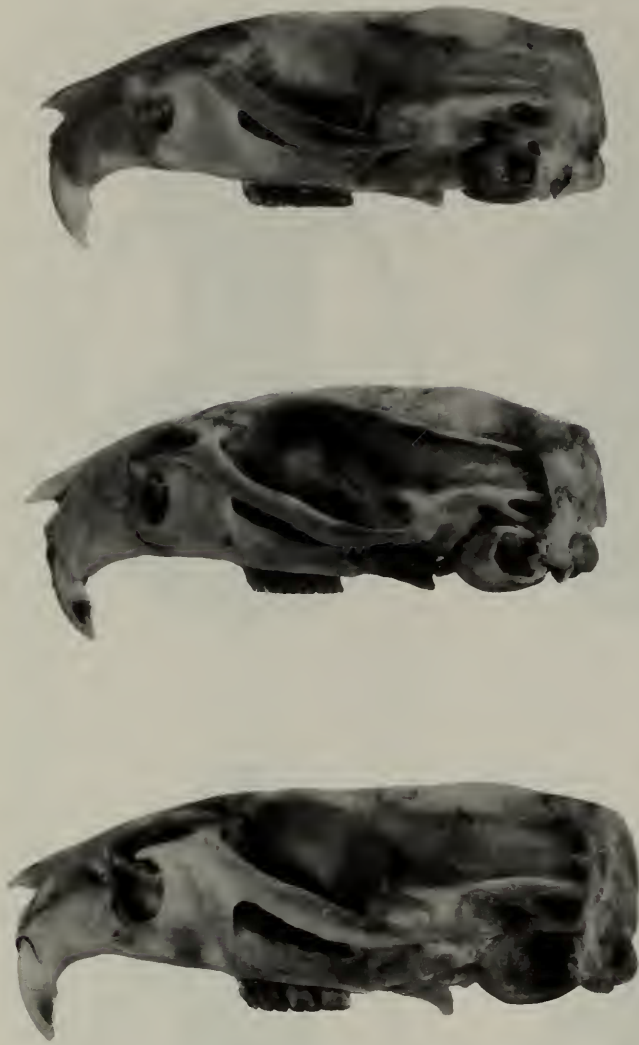


Fig. 4. Lateral cranial view of adult *Sigmodon*: top, *S. mascotensis*; middle, *S. hispidus berlandieri*; and bottom, *S. arizonae* (same specimen numbers as in Fig. 3).

rior and inferior temporal ridges (the latter called the occipital crest by Zimmerman 1970) provides a reliable means for discriminating examples of *S. hispidus* from those of *S. arizonae* and *S. mascotensis*. As noted by Zimmerman, this distance is visibly narrower in *S. hispidus* relative to the latter two (see Appendix), a difference underscored by our multivariate results in which distance between the temporal ridges (DTR) heavily influenced the separation of OTUs along the first canonical variate (Fig. 5, Table 4). The temporal ridges, together with the lateral arc of the transversely oriented lambdoidal ridge, define the size and shape of the temporal fossa, an area on the lateral wall of the braincase from which

originates the temporalis, an important masticatory muscle (Rinker 1954). In *S. hispidus* (and *S. alleni*), the temporal fossa tapers conspicuously toward the rear of the skull, forming a trapezoidal shape over the posterior half of the parietal and squamosal bones; whereas, the fossa in *S. mascotensis* and *S. arizonae* occupies a larger area, approximately rectangular in outline on the lateral braincase wall (Fig. 8). As expected for osseous features that provide muscular attachment, some change in fossa shape accompanies individual aging, such that juvenile animals of all three species exhibit a stronger rearward convergence of the superior and inferior temporal ridges; consequently, the size and shape differences noted are best appreciated when comparing crania of similar age classes.

The anterodorsal edge of the zygomatic plate forms a spinous process in all *Sigmodon* examined here, but its projection, and the degree of concavity imparted to the plate's anterior border, can aid specific identification, as demonstrated by Severinghaus and Hoffmeister (1978) for Arizonan populations of *S. hispidus* and *S. arizonae*. Among Nayarit samples, the spine is longest and most acute in specimens of *S. arizonae*, shortest in those of *S. alleni*. Configuration of the anterior zygoma in *S. mascotensis* more closely resembles *S. arizonae* but is not so extreme. Such interspecific contrasts are partially conveyed by certain variable loadings (BZP, LZS) generated from principal component and discriminant function analyses (Tables 3, 4), as well as by their mean differences (Appendix). Nevertheless, the expression of the spinous process has a strong age component (Table 2), which must be considered when comparing and identifying individuals. In *S. hispidus*, compared with *S. arizonae*, the spinous process is not only shorter, but its dorsal border appears wider and its tip is usually blunt (Severinghaus & Hoffmeister 1978:868, fig. 1; Hoffmeister 1986). In some individuals of *S. hispidus*, the spinous process is even expanded anteriorly to produce a knoblike

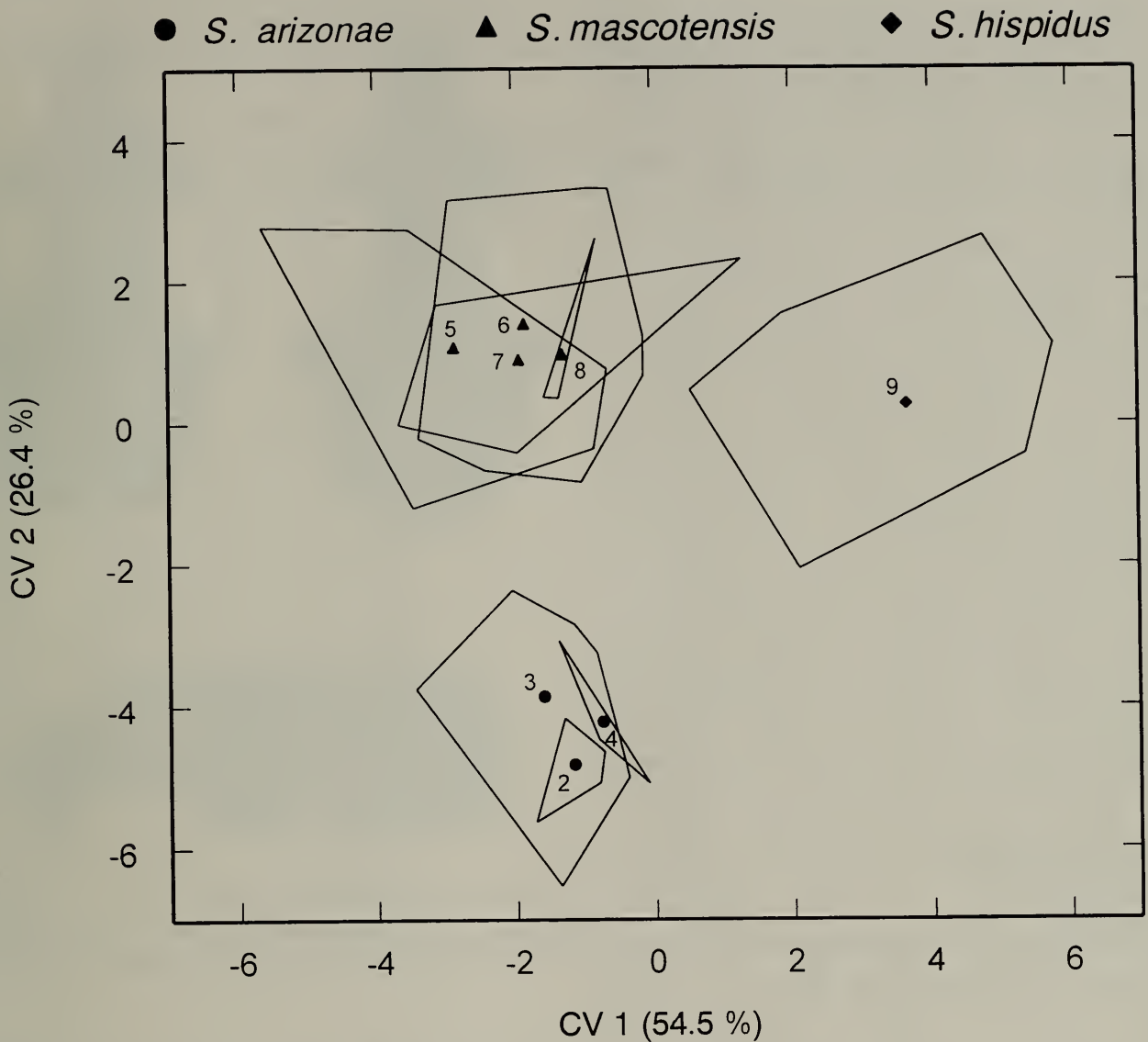


Fig. 5. Plot of the first and second canonical variates extracted from discriminant function analysis of eight samples of *Sigmodon arizonae* (OTUs 2–4), *S. mascotensis* (OTUs 5–8), and *S. hispidus* (OTU 9). Each of the eight OTU centroids is surrounded by a polygon that encloses maximal dispersion of sample scores. See Table 4.

tip. The contrast is similar in kind, if somewhat less pronounced in degree, between samples of *S. hispidus* and *S. mascotensis*.

The relative volume of the auditory bullae, difficult to capture accurately in a linear dimension (i.e., LAB) but easy to see in side-by-side comparisons of skulls, is another feature that separates *S. hispidus* from both *S. arizonae* and *S. mascotensis*—noticeably more inflated in the former and less so in the latter two (Fig. 3). Still, LAB contributed even more heavily than distance between the temporal ridges (DTR) to the segregation of the *S. hispidus* sample along

the first canonical variate (Fig. 5, Table 4). Voss (1992) characterized the auditory bullae of *S. hispidus* as “small,” but his taxonomic context involved contrast with the manifestly rotund capsules possessed by South American *S. peruanus*, a species indigenous to dry habitats in western Ecuador and northwestern Perú. Within the genus, the auditory bullae in members of the *S. hispidus* complex may be loosely graded as medium-sized, those of *S. alleni*, *S. arizonae*, and *S. mascotensis* as small, and those of *S. peruanus* as large.

The anatomy of the posterior palatal re-

Table 4.—Results of discriminant function analysis and one-way ANOVAs performed on eight OTUs representing intact specimens of *Sigmodon arizonae* ($n = 29$) and *S. mascotensis* ($n = 79$) from Nayarit, México, and *S. hispidus* ($n = 50$) from Florida, U.S.A. (see Fig. 5).

Variable	Correlations		ANOVAs f (OTU)
	CV 1	CV 2	
ONL	0.28	-0.57	15.8***
ZB	0.08	-0.74	19.4***
IOB	0.30	-0.35	3.9**
BBC	0.24	-0.67	13.9***
BOC	-0.19	-0.57	10.0***
DBC	-0.43	-0.58	16.8***
DTR	-0.58	-0.61	35.8***
LR	0.35	-0.53	14.1***
BR	0.13	-0.53	9.4***
PPL	0.19	-0.61	17.2***
LBP	0.38	-0.35	8.2***
BBP	0.33	-0.46	17.0***
LIF	0.40	-0.60	19.9***
LD	0.30	-0.55	14.1***
BZP	0.10	-0.36	5.4***
LZS	-0.03	-0.53	10.4***
LAB	0.77	-0.55	73.3***
LM1-3	0.22	-0.78	38.3***
WM1	0.21	-0.79	32.3***
DI	0.31	-0.43	7.7***
DM	0.33	-0.58	15.1***
Canonical correlations	0.94	0.89	
Eigenvalue	7.9	3.8	
% Variance	54.5	26.4	

** = $P \leq 0.01$; *** = $P \leq 0.001$.

gion affords several points of contrast that aid specific separation. In examples of *S. arizonae*, the palatine bones are distinctly keeled and terminate medially as a pronounced spine that projects into the mesopterygoid fossa (Fig. 9). A well formed mesopterygoid spine is atypical of *S. mascotensis* skulls (Figs. 9, 10), although the posterior border of their palatines may be gently curved or occasionally bluntly pointed. Even in the latter condition, however, the bony palate is relatively flat, unmarked by the conspicuous palatal gutters and raised keel observed in specimens of *S. arizonae*. The ventral opening of the foramen ovale, situated at the posterolateral corner of the parapterygoid fossa, is notably large in most *S. arizonae* and smaller in *S. mascotensis* (Figs. 9, 10). Although we opportunistically used a 0.9 mm-diameter probe

to convey this difference, some objective measure of foraminal area would better underscore the size distinction between the species. With regard to both palatal construction and size of the foramen ovale, the Floridian sample of *S. hispidus* resembles *S. arizonae*, but its variability is greater, at least according to the character states we have defined.

Another useful characteristic, one not mentioned by Zimmerman (1970) or Sevreringhaus & Hoffmeister (1978), involves the occurrence of an oval-shaped vacuity or fenestra on the parapterygoid fossa. Such an opening, situated just laterad to the pterygoid process and astride the palatine-ptyerygoid suture (Fig. 9), occurs commonly in samples of *S. mascotensis* (ca. 70%) but uncommonly in specimens of *S. arizonae* and *S. hispidus* (<25%). Nevertheless, this



Fig. 6. Dorsal, ventral, and lateral cranial views (about 1.75 \times) of an adult *Sigmodon alleni* (USNM 524479), a female from 4 km S Aticama, Nayarit.

character varies in all three species, so that the fenestra's presence or absence is not alone decisive for identification but informative when applied in combination with other qualitative and quantitative variables. In some individuals, especially those of *S. mascotensis*, the position of a presumptive fenestra is suggested by an oval area of thin, translucent bone ("Present, covered" per histogram, Fig. 11). By its location and orientation, the parapterygoid fenestra appears to correspond to the path of the anastomotic artery that crosses the dorsal surface of the pterygoid plate to supply the distal cephalic circulation in muroids having a reduced stapedia branch, as is true in most *Sigmodon* (Bugge 1970, Voss 1992, and see Carleton and Musser 1989: fig. 21). Why the impression of this artery's passage should usually ossify fully in some *Sigmodon* species but not in others is unknown;

the opening, however, does not appear to transmit nerves or blood vessels.

With regard to the typical conditions we reviewed above for *S. arizonae*, *S. hispidus*, and *S. mascotensis*, our series of *S. alleni* present an interesting mosaic of conditions. Like examples of *S. mascotensis*, the foramen ovale is small and the parapterygoid fenestra is typically present (on both sides in 10 individuals; one side in 2; and absent in 3); a mesopterygoid spine is usually present but small with shallow palatal corrugations. The temporal fossa, on the other hand, is narrow, convergent posteriorly in the manner of *S. hispidus*. The spinous process is short, slightly overhanging the zygomatic plate and tapering to a point (not wide and blunt as in *S. hispidus*). The auditory bullae of *S. alleni* are absolutely the smallest of the four species we have examined (Appendix) and in proportion nearly match the capsules of *S. mascotensis*.

As for other cranial features noted by Zimmerman (1978) or Severinghaus & Hoffmeister (1978), we subjectively assessed their variability apropos the Nayarit samples, but did not attempt to quantify their diagnostic utility because of their shape complexity or definitional arbitrariness (e.g., curvature of the lateral nasal margins, width of the presphenoid, shape of the occipital shield). Of these, the angularity (*S. hispidus*) or not (*S. arizonae* and *S. mascotensis*) of the dorsal rim of the occipital shield, as described by Severinghaus and Hoffmeister (1978), seems to provide consistent contrast, at least for the regional examples we examined.

Pelage color and texture.—Among the three species of Nayarit *Sigmodon*, *S. alleni* visually stands apart based on the uniformly rich brown color, occasionally with rufous- or cinnamon-brown tones, of its dorsal pelage. The common name, brown cotton rat, is aptly descriptive of the species. Rufescent tints are most evident over the rump, with medium brown on the middle dorsum that fades on the flanks to create a paler tawny hue. In texture, the dorsal fur of *S.*

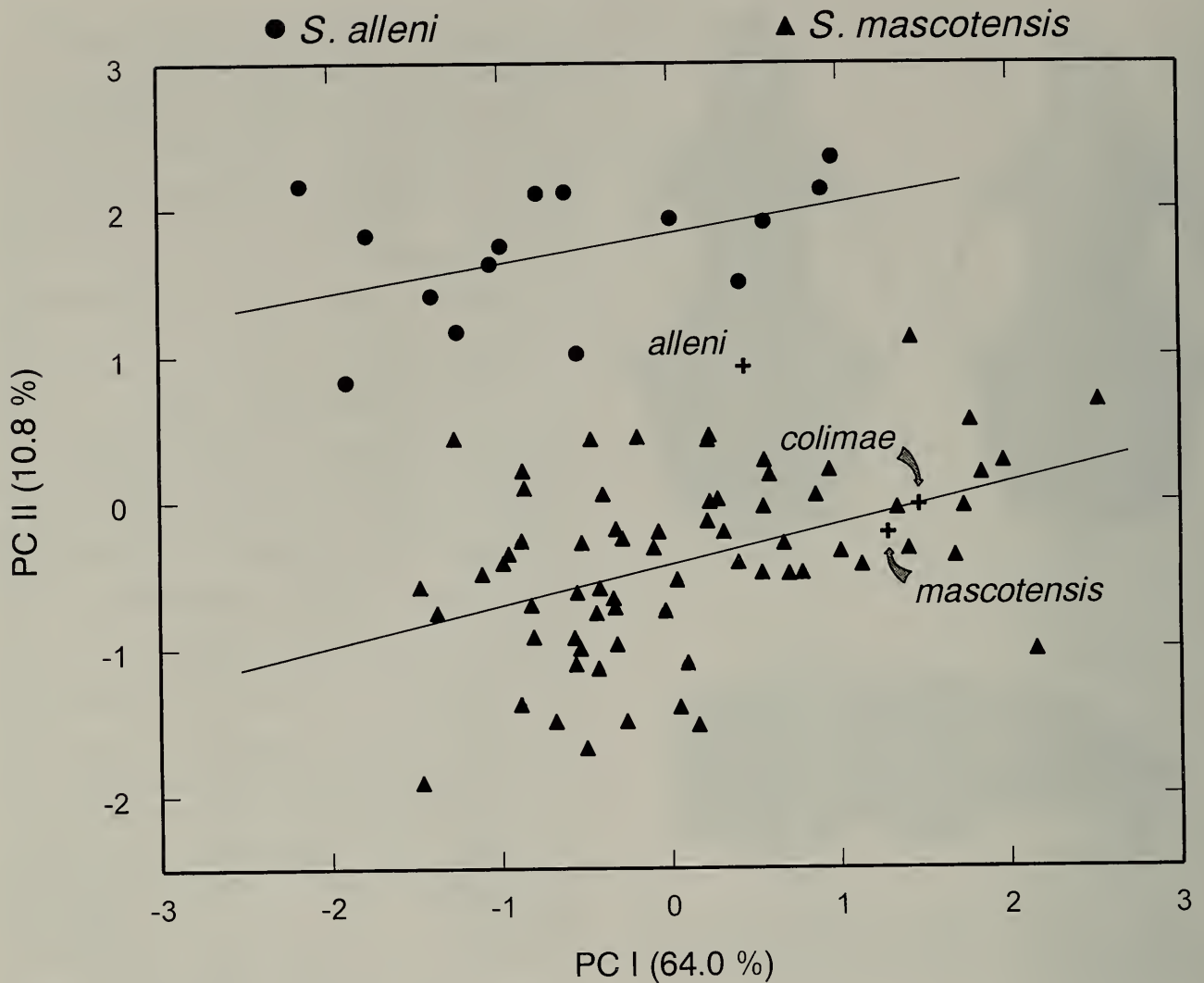


Fig. 7. Plot of first and second principal components extracted from analysis of 21 log-transformed craniodental variables measured on intact specimens of Nayarit *Sigmodon alleni* ($n = 15$) and *S. mascotensis* ($n = 79$). Crosses indicate relevant type specimens discussed in the text. Regression lines of PC II on PC I differ significantly between species in their y-intercepts (1.84 versus -0.42 ; $F = 156.0$, $P < 0.001$) but not their slopes (0.18 versus 0.28; $F = 0.4$, $P = 0.544$). See Table 5.

alleni is comparatively soft and fine, only slightly stiff to the touch; guard hairs on the rump are mostly unicolored and project little above the cover hairs.

The upperparts of *S. mascotensis* and *S. arizonae* suggest some shade of brown: typically a paler saturation, brighter tone, and distinctly grayish hue in the former species; and a darker saturation, more somber cast, and yellowish hue in the latter. In specimens of *S. arizonae*, there is greater intermixture of darkly tipped cover hairs over the mid-dorsum, which contrasts more noticeably with the yellow browns of the flanks; in examples of *S. mascotensis*, the grayish brown pelage color is usually even-

ly expressed across the dorsum. The subtle difference in shade of brown also results from the band colors of their agouti-patterned cover hairs: the basal band a pale plumbeous gray and middle band medium buff in *S. mascotensis* versus a dark gray basal band and deep buff middle band in *S. arizonae*. The chromatic accent of the buffy middle bands against the darker bases and tips of the cover hairs imparts a more grizzled or flecked appearance to the upperparts of *S. arizonae* and *S. mascotensis*; in individuals of *S. alleni*, the middle band is ochraceous and less dramatically set off from the umber tips. In further contrast to *S. alleni*, the dorsal fur in the two larger

Table 5.—Results of principal component analysis and one-way ANOVAs performed on all intact specimens of *Sigmodon alleni* ($n = 15$) and *S. mascotensis* ($n = 79$) from Nayarit, México (see Fig. 7).

Variable	Correlations		ANOVAs f (species)
	PC I	PC II	
ONL	0.93	0.24	0.5
ZB	0.95	0.01	11.5**
IOB	0.48	0.27	0.8
BBC	0.73	-0.03	9.6**
BOC	0.44	-0.10	6.7*
DBC	0.61	-0.43	51.1***
DTR	0.78	-0.44	48.5***
LR	0.85	0.39	0.5
BR	0.82	0.37	1.0
PPL	0.90	0.26	0.5
LBP	0.44	0.17	0.0
BBP	0.85	0.03	5.5*
LIF	0.87	0.19	2.6
LD	0.89	0.36	0.0
BZP	0.85	0.08	3.0
LZS	0.77	-0.44	47.1***
LAB	0.67	-0.13	12.1**
LM1-3	0.42	-0.49	46.4***
WM1	0.43	-0.52	56.6***
DI	0.87	0.17	2.1
DM	0.90	0.23	0.4
Eigenvalue	0.073	0.012	
% Variance	64.0	10.8	

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

species is coarser and sparser, especially so in *S. arizonae*, and can be tactually appreciated as hispid. Guard hairs are conspicuously longer than the cover hairs over the rump and consist of both monocolored black and agouti-banded types.

Ventral cover hairs of all three species are bicolored, having a plumbeous gray base and a pale tip. The general appearance of the ventrum and the color differences observed between species principally depends upon the pigmentation of the tips. In *S. alleni*, the tips are buffy to pale ochraceous and the bases dull plumbeous, imparting a somber, dark gray color to the venter. In *S. mascotensis*, the cover hairs terminate in pure white, creating a light gray impression and conveying brighter tones than the underparts of the other species, especially *S. alleni*. Ventral pelage color is more variable in *S. arizonae*; some individuals have a predominance of pale buffy tips, while in others they are dull white. The overall impression is one of dull to medium gray, in contrast to the brighter grays of *S. mascotensis*.

The upper surfaces of the hindfeet are generally well haired in all three species but

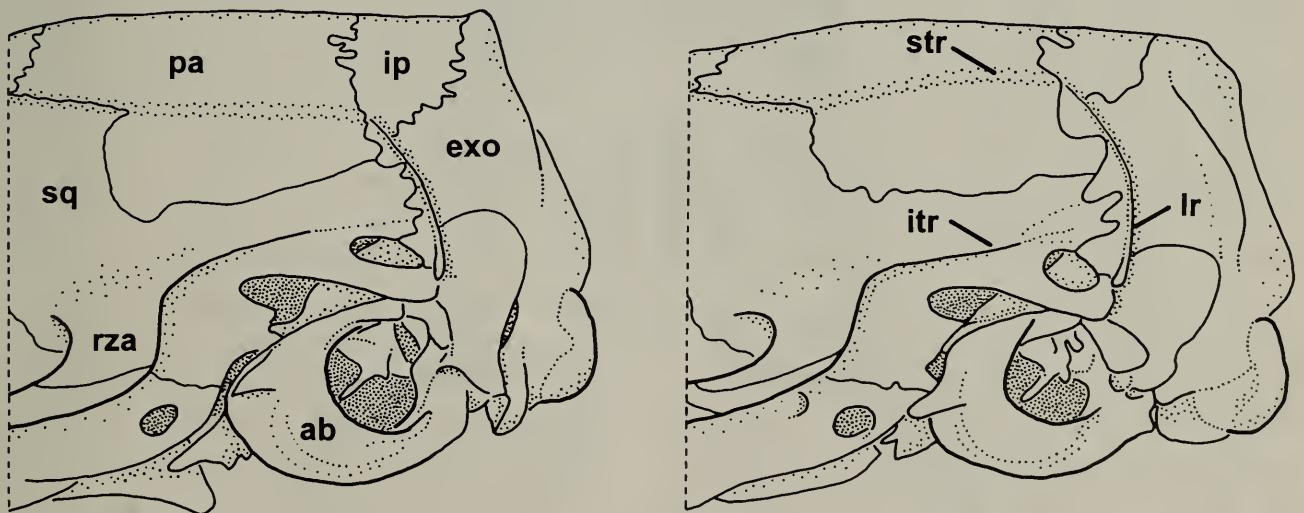


Fig. 8. Left lateral view of the temporal region in adult examples of *Sigmodon hispidus* (left; USNM 526071, Florida, St. Marks National Wildlife Refuge) and *S. mascotensis* (right; USNM 523954, Nayarit, 8 mi S Ahuacatlán). Abbreviations: ab, auditory bullae; exo, exoccipital; ip, interparietal; itr, inferior temporal ridge; lr, lambdoidal ridge; pa, parietal; rza, squamosal root of the zygomatic arch; sq, squamosal; str, superior temporal ridge. The superior temporal, inferior temporal, and lambdoidal ridges outline a trapezoidal shape of the temporal region in *S. hispidus* in contrast to the rectangular shape observed in *S. arizonae* and *S. mascotensis*. The distance between the temporal ridges (DTR) was measured between the points of the arrows denoting the superior (str) and inferior (itr) ridges.

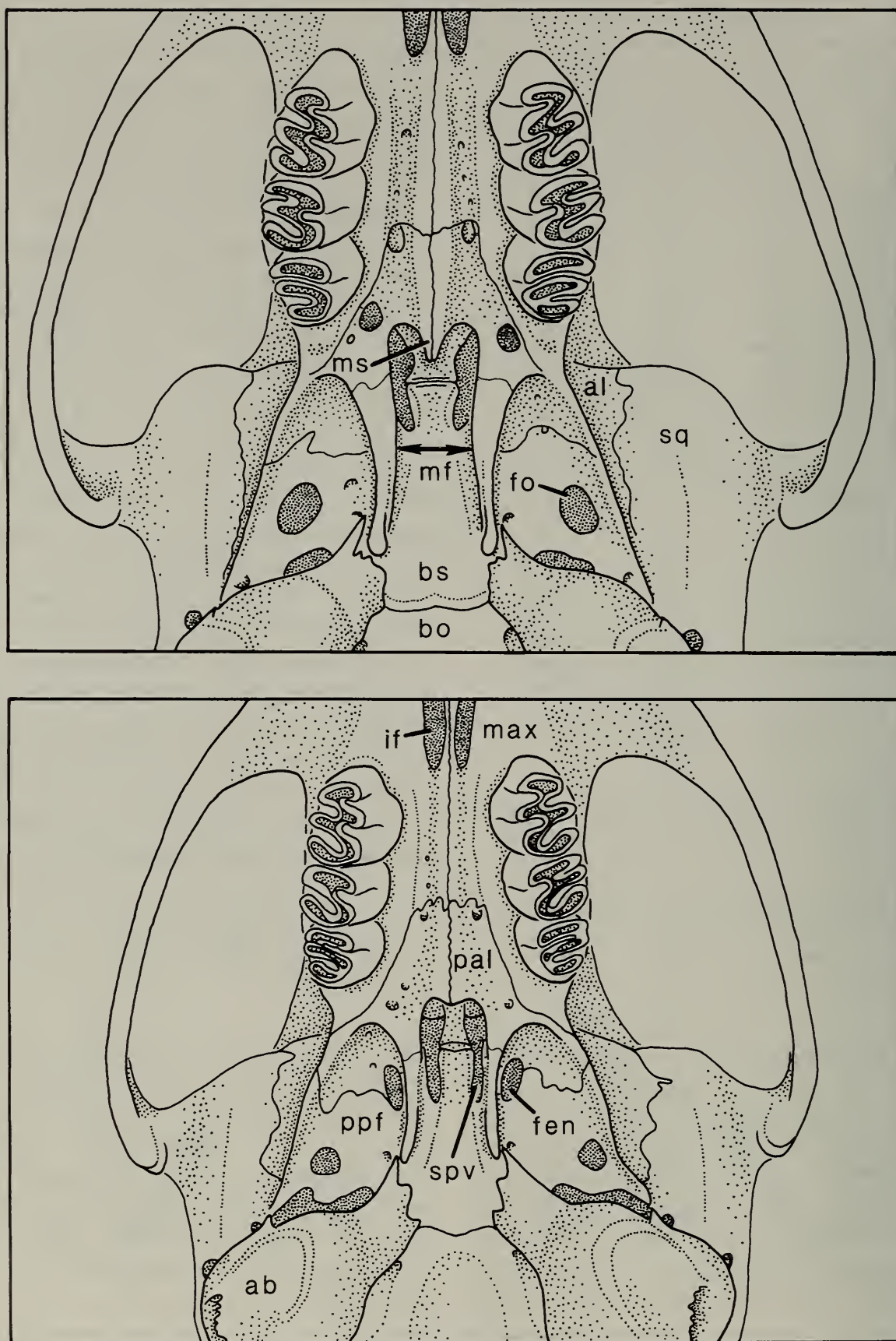


Fig. 9. Ventral view of the bony palate and adjoining parapterygoid and mesopterygoid fossae in Nayarit examples of *Sigmodon arizonae* (top; USNM 510012, 2 mi E San Pedro Lagunillas) and *S. mascotensis* (bottom; USNM 510022, 2 mi E San Pedro Lagunillas). Abbreviations: ab, auditory bullae; al, alisphenoid bone; bo, basioccipital bone; bs, basisphenoid bone; fen, fenestra of parapterygoid fossa; fo, foramen ovale; if, incisive foramen; max, maxillary bone; mf, mesopterygoid fossa; ms, mesopterygoid spine; pal, palatine bone; ppf, parapterygoid fossa; spv, sphenopalatine vacuity; sq, squamosal bone. In *S. arizonae*, as compared with *S.*

chromatic differences are apparent. Hairs covering the dorsal metatarsus and phalanges of *S. alleni* have dusky bases with buffy to pale ochraceous tips, such that hindfoot color generally blends with the reddish-brown appearance of the dorsum. Like the hairs of its ventral pelage, those on the hindfeet of *S. mascotensis* have plumbeous gray bases and bright white tips; thus, the feet appear pale gray and distinctly contrast with the grayish browns of the rump. Upper surfaces of the hindfeet of *S. arizonae* appear medium gray to dull brown over the metatarsum and grayer on the phalanges, blending with the dorsum more so than in *S. mascotensis* but less so compared with *S. alleni*.

Although Bailey (1902) characterized all of these taxa as having semi-naked and coarsely annulated tails, we found clear differences in caudal pilosity and scutellation. Epidermal scales appear dark brown, above and below, in all three; consequently, expression of bicolouration issues from the interplay of hair color, density, and length. None of the species, however, possesses a truly bicolored tail (e.g., like that of *Peromyscus maniculatus*) with sharp linear demarcation between dark dorsal and pale ventral surfaces. Instead, transition from darker dorsal to the paler undersurface is gradual. In examples of *S. alleni*, the tail is sparsely covered, the caudal hairs extending over 2–3 annuli; the color is dark brown dorsally and slightly paler below, bicolouration weakly expressed and effectively unicolor in some individuals; caudal scales are small but typically visible to the naked eye given the relatively sparse investiture of hairs. Individuals of *S. mascotensis* possess a similarly fine scalar pattern, but caudal hairs are longer, about 4 annuli in length, and scutellation is mostly obscured. This

species most nearly approaches a bicolored condition, brown above and pale gray below. In samples of *S. arizonae*, the tail is dark brown above and grades imperceptibly to paler brown below. Caudal scales are noticeably larger, and the annulations accordingly coarser and readily evident macroscopically. Paradoxically, the annulation pattern remains visibly appreciable in *S. arizonae* even though its caudal hairs are absolutely longer (about 4–5 annuli) in contrast to those of *S. mascotensis*. The impression of semi-nakedness arises from the sparser density of caudal hairs, arranged in triplets as in the other species but more widely spaced as a result of the larger tail scales.

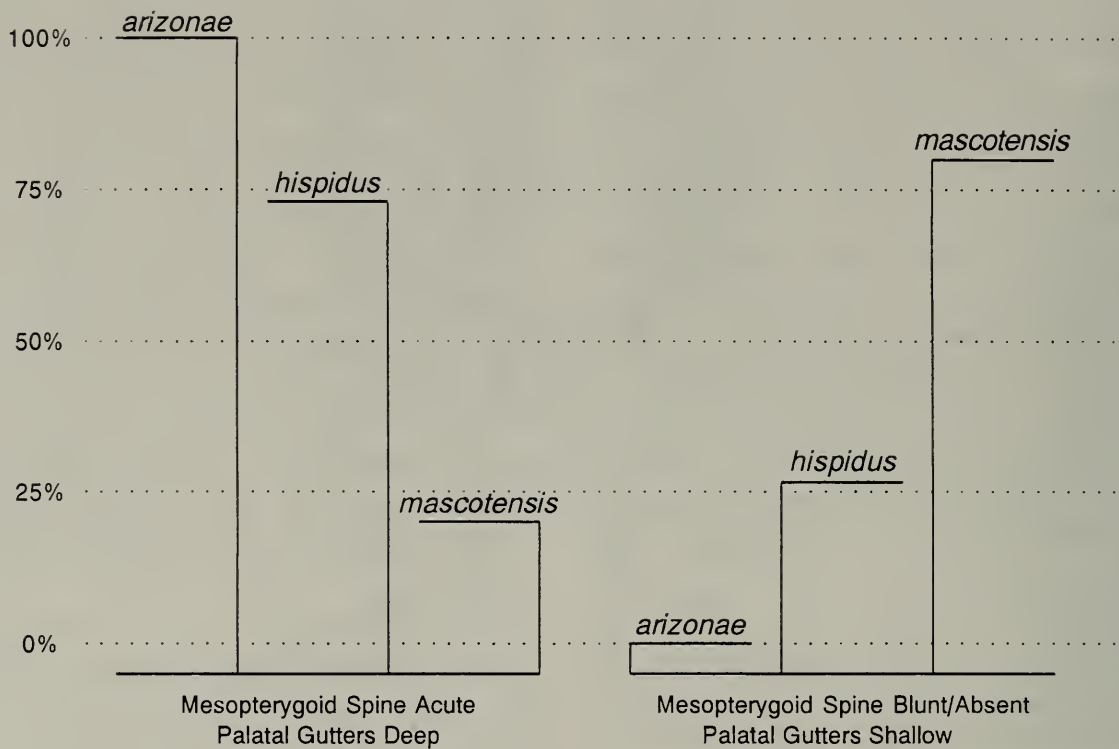
Chromosomal variation.—Three well marked chromosomal formulae are apparent among Nayarit *Sigmodon*. The diploid number (2N) of *S. arizonae* is 22, consisting of largely biarmed chromosomes (fundamental number, FN, = 38). The autosomes number four pairs of very large metacentrics and submetacentrics, two pairs of large subtelocentrics, two pairs of medium-sized metacentrics, one pair of small submetacentrics, and a single pair of small acrocentrics (Fig. 12). The X chromosome is a medium-sized acrocentric; the Y, a small acrocentric with discernible secondary arms, is the smallest element in the complement. This karyotype is identical to that described by Zimmerman (1970) for the 22-chromosome cotton rats he studied from Arizona, Sinaloa, and Nayarit.

The diploid number in examples of *S. mascotensis* is invariantly 28, nearly all of the autosomes uniarmed (FN = 28). Autosomes consist of 12 pairs of acrocentrics, gradated in size from medium to large, and one pair of small subtelocentrics (Fig. 12). The X chromosome is a medium-sized ac-

←

mascotensis, note the occurrence of a pronounced mesopterygoid spine, the conspicuously larger size of the foramen ovale, and the absence of a parapterygoid fenestra.

CONDITION OF BONY PALATE



SIZE OF FORAMEN OVALE

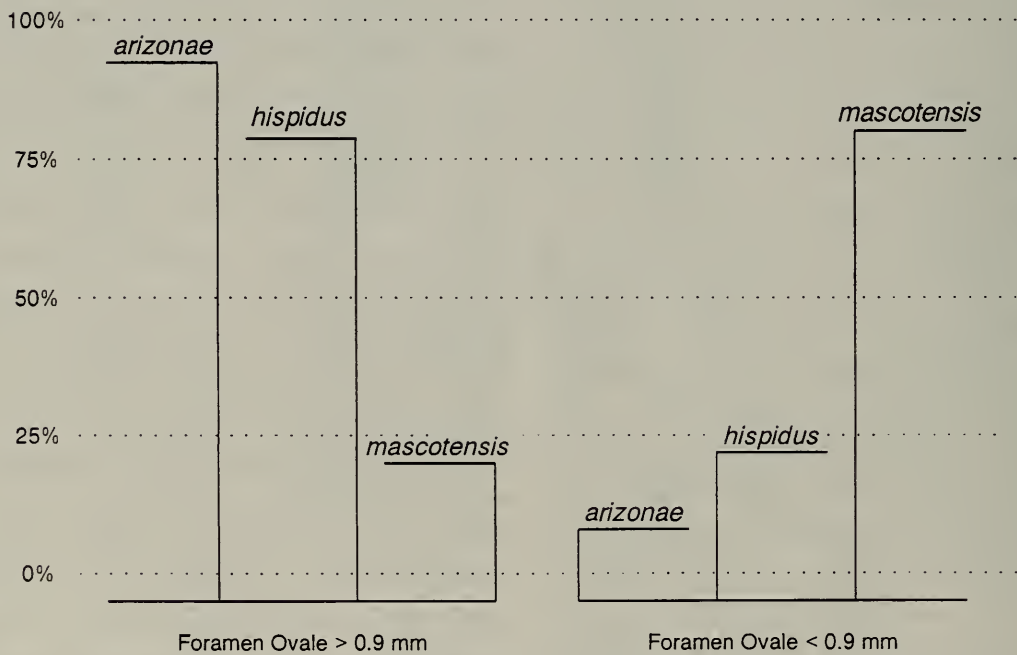


Fig. 10. Percent occurrence of certain qualitative cranial characters in samples of *Sigmodon arizonae* ($n = 36-40$) and *S. mascotensis* ($n = 88-91$) from Nayarit, México, and in *S. hispidus* ($n = 53$) from Florida, U.S.A. Top, condition of the bony palate; bottom, size of the foramen ovale (See Fig. 9 for illustration and text for description of character states).

PATENCY OF PARAPTERYGOID FENESTRA

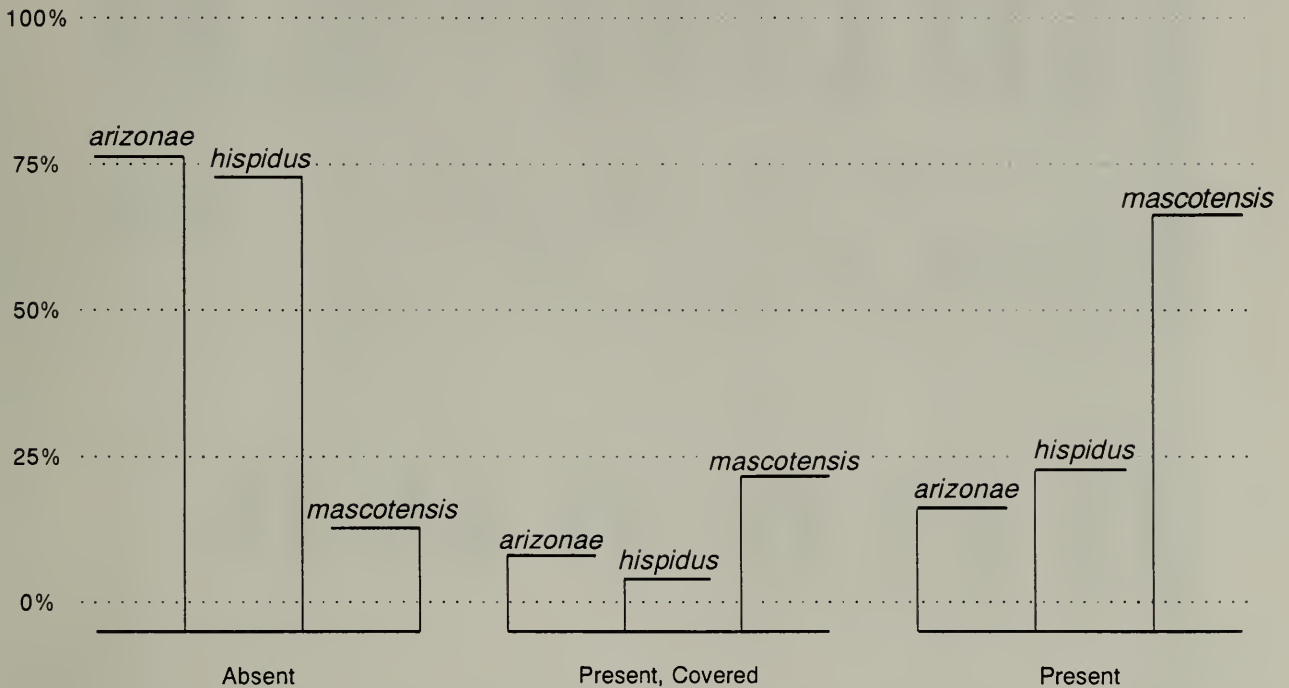


Fig. 11. Percent occurrence of character states of the right parapterygoid fenestra in samples of *Sigmodon arizonae* ($n = 38$) and *S. mascotensis* ($n = 86$) from Nayarit, México, and in *S. hispidus* ($n = 52$) from Florida, U.S.A. (See Fig. 9 for illustration and text for description of character states).

rocentric; the Y, a tiny acrocentric, is smaller than any of the autosomal acrocentrics. A female (USNM 511706) from Rancho Sapotito is heteromorphic for a centric fusion involving two similarly sized larger acrocentrics; two other females and two males karyotyped from this locality possess typical karyotypes. Lee & Zimmerman (1969) noted similar examples of heteromorphic karyotypes resulting from centric fusion in *S. fulviventer*, and Zimmerman (1970) reported the same phenomenon in *S. hispidus*.

Zimmerman (1970) characterized all autosomes in *S. mascotensis* as acrocentric (that is, FN = 26), but we follow Elder (1980) in describing the smallest of these as subtelocentric (FN = 28). In most spreads, this pair has clearly discernible second arms (see Fig. 12), which Elder (1980) found to be heterochromatic in most of his C-banded preparations. Excepting this minor discrepancy in autosomal classification, the karyotype of Nayarit animals

conforms to those described by Zimmerman (1970) from scattered localities in southern Jalisco, Michoacán, Guerrero, and western Oaxaca.

In *S. alleni*, the 2N is consistently 52 and the FN is typically 64. Autosomes in the 64-FN karyotype consist of one pair of large, four pairs of medium-sized, and one pair of small subtelocentrics; one pair of very small metacentrics; and 18 pairs of acrocentrics graded in size from small to medium (Fig. 13). At Lo de Marcos, two FNs, 64 and 66, are apparent. The autosomal complement in the 66-FN karyotype includes an additional pair of small submetacentrics and lacks a pair of acrocentrics. The X chromosome is a moderately large subtelocentric; the Y is a small subtelocentric. The karyotype Zimmerman (1970) reported for *S. alleni* from Michoacán is similar to our 64-FN pattern, except that the Y chromosome in our Nayarit samples appears to be smaller.

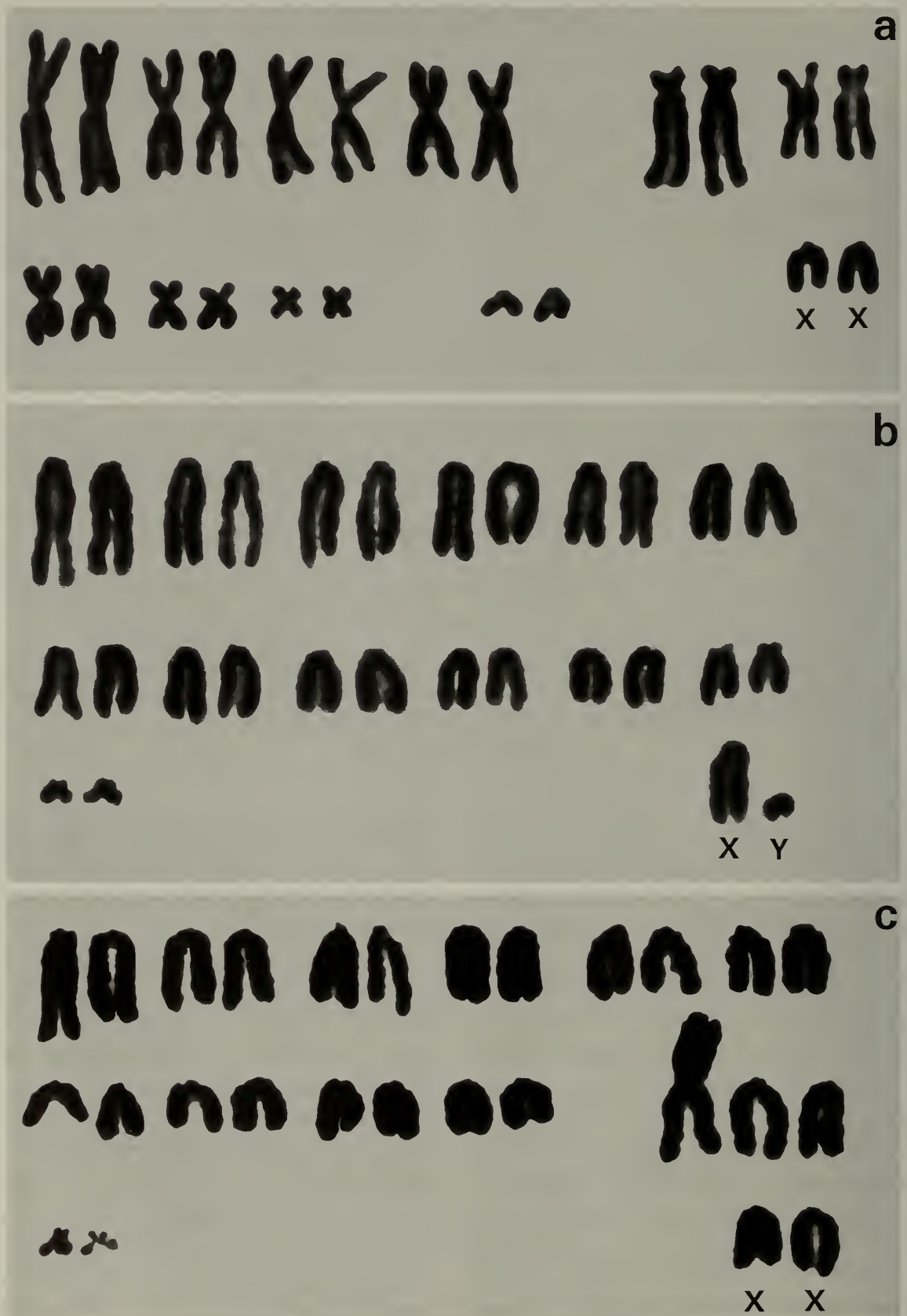


Fig. 12. Representative karyotypes of Nayarit *Sigmodon*: a, *S. arizonae* (USNM 511700), a female from Mesa del Nayar; b, *S. mascotensis* (USNM 523953), a male from 8 mi S Ahuacatlán; c, heteromorphic variant of *S. mascotensis* (USNM 511706), a female from Rancho Sapotito.

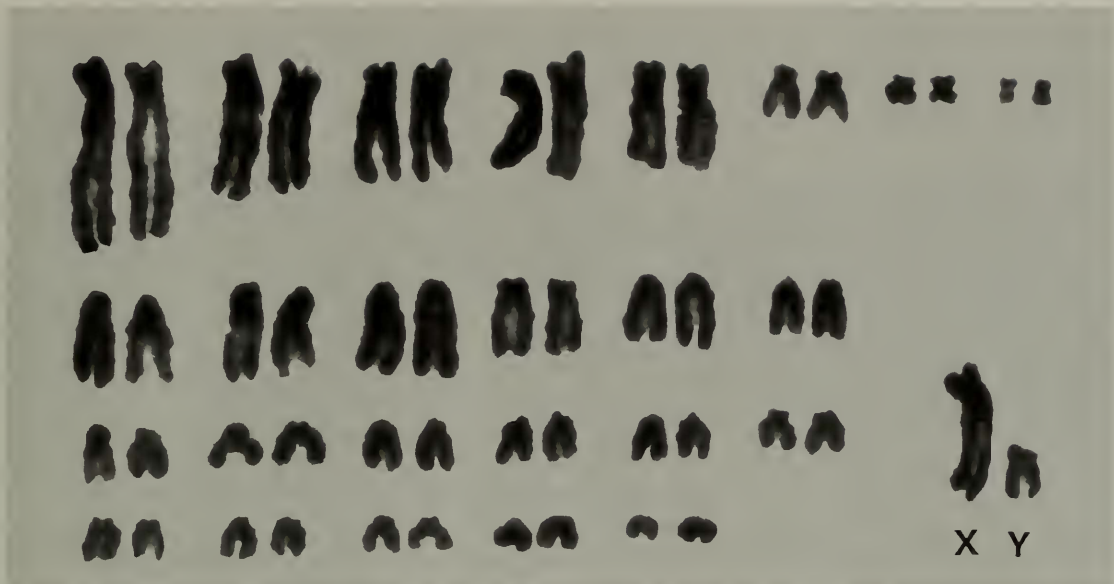


Fig. 13. Representative karyotype of *Sigmodon alleni* (USNM 523940), a male from 1 mi S Lo de Marcos.

Discussion

Bailey's (1902) revision of *Sigmodon* established the view that most North American populations with coarsely annulated, partially naked tails are geographic races of *S. hispidus*, including the distinctive complex of large-bodied cotton rats found in the southwestern U.S.A. and western México. His classification prevailed over subsequent decades and accommodated most new descriptions of taxonomic variety as subspecies (Miller 1924, Miller & Kellogg 1955, Hall & Kelson 1959). Zimmerman's (1970) fine synthesis of chromosomal and morphological information abruptly overturned this comfortable arrangement and resurrected both *S. arizonae* and *S. mascotensis* as valid species distinct from *S. hispidus*. The morphological basis for specific stature of these forms was amplified by Severinghaus & Hoffmeister (1978) and Hoffmeister (1986), who also refined our understanding of their intermingling distributions in the southwestern U.S.A. and northwestern México. Morphometric, morphological, and chromosomal differences observed among Nayarit populations of *Sigmodon* further corroborate the taxonomic insights and nomenclatural realignments advanced by Zimmerman (1970).

Examples of *S. alleni*, *S. arizonae*, and

S. mascotensis were collected in all possible pairwise combinations of sympatry, but at no place were all three species documented. Of particular note is the co-occurrence now recorded for *S. arizonae* and *S. mascotensis* at a locality east of San Pedro Lagunillas in southcentral Nayarit. Although collected "sympatrically" in terms of bearing a single skin-tag provenience, the two species are apparently segregated according to microhabitat at this place. The vegetation in the vicinity includes succulent dicots, particularly water hyacinth, and marsh grasses bordering the small lake; and dryer brush, low sparse woodland, and bunchgrasses covering the hillsides that overlook the lake (Fig. 14). Most examples of *S. arizonae* originated from the former habitat and those of *S. mascotensis* from the latter (Fig. 15). Whether the two species at this place are entirely nonoverlapping in their microhabitat occurrence is unknown, since field identifications were tentative at the time of collection. Furthermore, whether the specific habitat affinities recorded at this one locality reflect general ecological differences of the species, particularly their humidity tolerances, will require extended site investigations.

The distinctive cranial and pelage features so apparent in Nayarit *S. mascotensis*



Fig. 14. Panoramic view of collecting site at the eastern side of the small lake San Pedro Lagunillas and two miles east of the village of the same name. Traplines were placed both along the emergent lakeside vegetation and on the dryer hillside and tableland.

encouraged our review of its distribution in western México. We concur with all species-group epithets so far allocated to the species by Zimmerman (1970) and Hall (1981): these are *atratus*, *colimae*, *inexoratus*, and *ischyrus*. Like Allen's (1897b) *S. mascotensis*, populations represented by each of these names are large, grayish brown cotton rats with strongly hispid fur and relatively long tails; their crania possess relatively small auditory bullae and expansive temporal fossae; the occurrence of parapterygoid fenestrae is common within locality samples, but a large foramen ovale, pronounced mesopterygoid spine, and deep palatal grooves are uncommon. The forms *tonalensis* Bailey (1902) and *obvelatus* Russell (1952), currently maintained as subspecies of *S. hispidus* (Hall 1981, Musser & Carleton 1993, Alvarez-Castañeda 1996), also fit well with this morphology

and properly belong as junior synonyms of *S. mascotensis* (see remarks under Taxonomic Summary).

The emergent picture of *S. mascotensis* distribution reveals a species confined to western México, documented from southern Nayarit and Zacatecas to extreme western Chiapas (Fig. 16). Although its range boundaries appear convoluted and constituent populations are certainly discontinuous, the occurrence of the species corresponds closely to deciduous or semideciduous tropical woodlands having a pronounced dry season. Comments by collectors typically mention the semiarid to arid environment and-or xerophilous vegetational character of localities where *S. mascotensis* has been captured (Hooper 1947, 1957; Goldman 1951; Russell 1952; Goodwin 1969; Alvarez et al. 1987). According to Goldman's (1951) life-zone di-



Fig. 15. Microhabitat preferences of *Sigmodon* captured at 2 mi E San Pedro Lagunillas (see Fig. 14). Top: hillside covered with brush, low broken woodlands, and bunch grasses where examples of *S. mascotensis* were captured. Bottom: dense growth of water hyacinth fringing the lake and inhabited by *S. arizonae*.

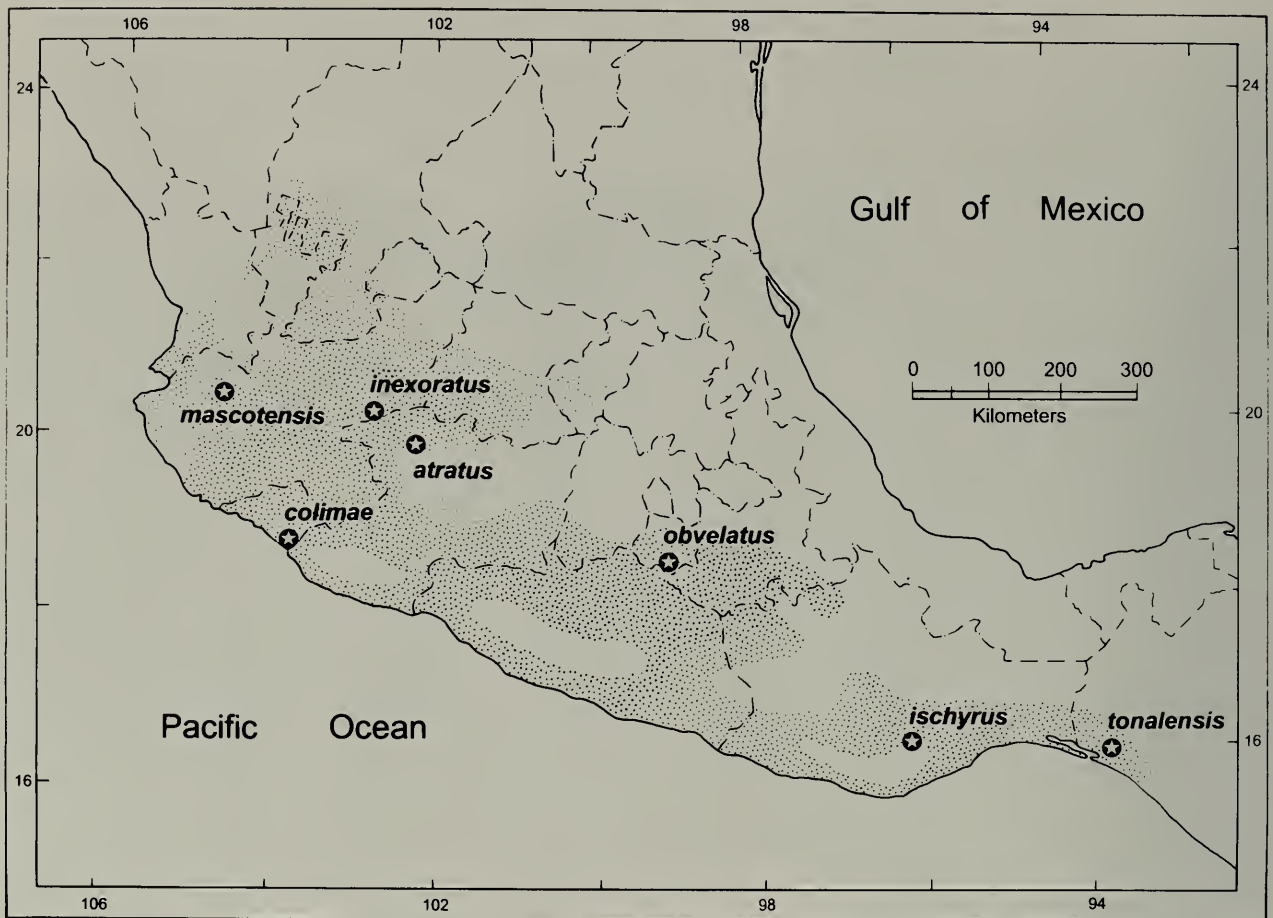


Fig. 16. Generalized distribution of *Sigmodon mascotensis* in western México based on specimens examined herein. Enclosed stars identify the type localities of the six species-group taxa that we view as regional synonyms of *S. mascotensis* Allen (1897), including two newly associated herein (*tonalensis* Bailey, 1902, and *obvelatus* Russell, 1952).

visions of México, nearly all of these distributional records represent either Arid Lower Tropical Subzone or Arid Upper Tropical Subzone, a few the Lower Austral Zone; by Leopold's (1959) categorization of broad vegetational units, they fall within Tropical Deciduous Forest and Arid Tropical Scrub. Not unexpectedly, in view of such climatic and vegetational associations, the geographic boundary of the species conforms well to certain biotic patterns distilled from distributions of the Mexican herpetofauna (Flores-Villela 1993).

The range of *S. mascotensis* collectively overlies three physiographic regions: Pacific coastal plain and the contiguous lowlands of the Isthmus of Tehuantepec; the drainage basin and surrounding tablelands of Lago de Chapala (Meseta Central de Anáhuac or Altiplano Sur), including the Tequisquiapan

Valley; and the Balsas Basin, including the Tehuacán Valley. Except for those records in the Tehuacán valley of western Puebla, collecting sites of *S. mascotensis* predominantly occur within hydrologic systems that ultimately drain into the Pacific Ocean; the Río Salado of the Tehuacán Valley joins the Río Santa Domingo, a major effluent to the Gulf of México. The Tehuacán-Cuicatlán Valley is presently considered part of the same physiographic domain as the Balsas Basin (Sierra Madre del Sur Morphotectonic Province), but persuasive argument for past biotic connections drawn from geological evidence is elusive, given both the daunting complexity of México's physical landscapes and the continuing need for geologic-tectonic research (see review by Ferrusquía-Villafranca 1993).

Although our study is focussed on means

for interspecific discrimination, we are as much impressed by the morphological similarities that *S. arizonae* and *S. mascotensis* share, notably the configuration of the temporal fossa and degree of bullar inflation. Goodwin (1969:199) had earlier appreciated the fundamental affinity among these populations and summarized their external resemblances: “*Sigmodon h. mascotensis* is in a group of several subspecies of very large, long-tailed, coarse-haired cotton rats that range from Arizona [i.e., *arizonae*] in western North America south along the slopes and plains of the Pacific coast in México to Tonalá, Chiapas.” Such general notions of kinship, along with their geographically complementary distributions, suggest a sister-group relationship, a hypothesis which has received more rigorous endorsement from traditional and banding chromosomal studies (Zimmerman 1970, Zimmerman & Sihvonen 1973, Elder 1980). Zimmerman (1970), for example, divided North and Middle American *Sigmodon* into two species groups based on a combination of diploid and fundamental numbers: those with a low range ($2N = 22-30$, $FN = 26-38$), consisting of *S. arizonae*, *S. fulviventer*, and *S. mascotensis*; and those with a high range ($2N = 52-56$, $FN = 52-66$), consisting of *S. alleni*, *S. hispidus*, *S. leucotis*, and *S. ochrognathus*. Assuming derivation from a *S. hispidus*-like ancestor, G-banding evidence supports the common ancestry of *S. arizonae* and *S. mascotensis* (Elder 1980). The phyletic affinity of *S. fulviventer* with *S. arizonae* and *S. mascotensis* as postulated by Zimmerman (1970) remains untested.

More importantly, our nomenclatural and distributional amendments of *S. mascotensis* bear on a taxonomically more entangled issue: what is *S. hispidus* proper? As now documented, populations of medium to large *Sigmodon* known to occur throughout the Pacific coastal lowlands and west-facing slopes from Sonora to western Chiapas, represent either the species *S. alleni*, *S. arizonae*, or *S. mascotensis*. Supposed west-

ern records for *S. hispidus* proper have proven incorrect upon reexamination. Specimens from Jalisco and Querétaro that had been assigned to *S. h. berlandieri* (Bailey 1902, Hall 1981) are in fact *S. mascotensis*, as enumerated below in the Taxonomic Summary; Goodwin’s (1969) two vouchers (KU 63075, 63076) of *S. h. saturatus* in southern Oaxaca (1 mi NNW Soledad) are instead *S. alleni*, as corrected by Baker (1969). To our knowledge, these reidentifications, together with reallocation of *obvelatus* and *tonalensis* and their referred series, remove any documentation for *S. hispidus* along the entire Pacific versant of México.

The inability of discriminant coefficients to associate Middle American holotypes of nominal “*hispidus*” with Floridian *S. hispidus* indirectly attests the still composite nature of the species as arranged. While our selection of this Floridian population sample as a standard for *S. hispidus* proper was a reasonable choice, on geographic and morphologic grounds, our expectation of its agreement with Neotropical taxa proved wonderfully naive. Most holotypes representing such populations clustered among or nearer the Nayarit samples of *S. mascotensis* (Fig. 17) and were classified a posteriori with that species (Table 6). None of these numerically probabilistic assignments, except Bailey’s (1902) *tonalensis*, merits serious consideration as biological truth—the various taxa are not conspecific with *S. mascotensis* of western México. Those craniodental variables that heavily influenced multivariate separation among centroids—particularly LAB on the first canonical variate and LM1-3 and WM1 on the second—are small in most of the Middle American type specimens, as compared with typical *S. hispidus* (OTU 9). By default these were associated with examples of *S. mascotensis*, since among the eight predefined OTUs, individuals of that species possess the smallest bullae, shortest tooththrows, and narrowest molars compared with typical *S. hispidus* or *S. arizonae* (Ap-

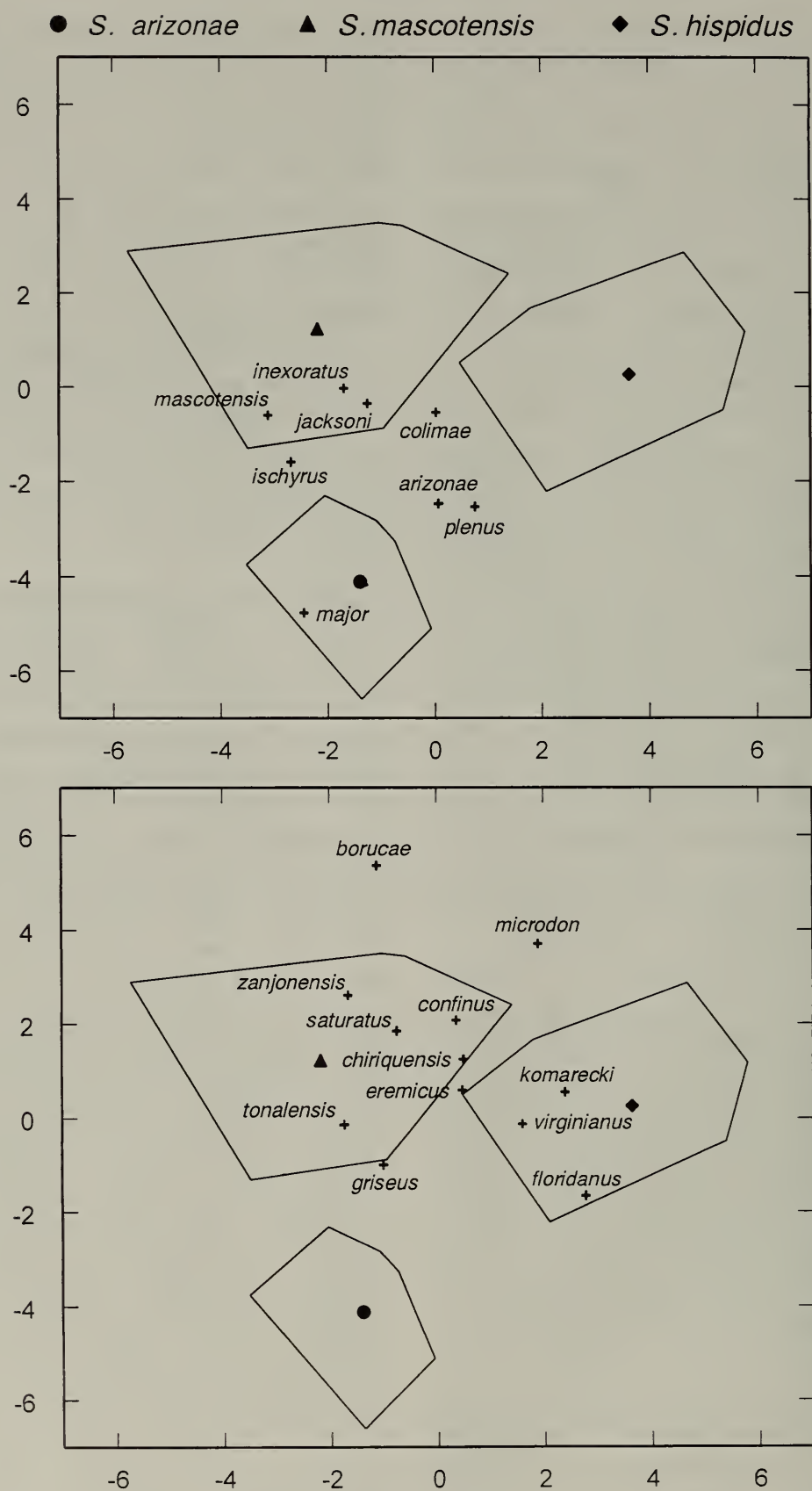


Fig. 17. Phenetic dispersion of type specimens of *Sigmodon* based on discriminant coefficients extracted from the same discriminant function analysis of eight samples of *Sigmodon arizonae* (OTUs 2–4), *S. mascotensis* (OTUs 5–8), and *S. hispidus* (OTU 9). Polygons in this instance enclose the maximal dispersion of all specimen scores around the grand centroid for each species (compare with Fig. 5). Top, type specimens of forms currently considered synonyms of *S. arizonae* (*jacksoni*, *plenus*, and *major*) and *S. mascotensis* (*colimae*, *inexoratus*, and *ischyurus*); bottom, type specimens of forms currently considered synonyms of *S. hispidus* (two groups plotted separately to avoid visual congestion). See Table 6 and text for discussion.

Table 6.—A posteriori classification of type specimens of *Sigmodon* derived from discriminant function analysis of OTUs 2–9 (see Fig. 17).

Holotype	Current classification	A posteriori OTU assignment	P
<i>arizonae</i> Mearns (AMNH 2370/1841)	<i>S. arizonae</i>	2 (<i>arizonae</i>)	0.71
<i>major</i> Bailey (USNM 96275)	<i>S. arizonae</i>	2 (<i>arizonae</i>)	0.99
<i>jacksoni</i> Goldman (USNM 214121)	<i>S. arizonae</i>	5 (<i>mascotensis</i>)	1.00
<i>plenus</i> Goldman (USNM 181086)	<i>S. arizonae</i>	3 (<i>arizonae</i>)	1.00
<i>mascotensis</i> Allen (AMNH 8321/6655)	<i>S. mascotensis</i>	8 (<i>mascotensis</i>)	1.00
<i>colimae</i> Allen (AMNH 2648/2318)	<i>S. mascotensis</i>	7 (<i>mascotensis</i>)	0.67
<i>inexoratus</i> Elliot (FMNH 8651)	<i>S. mascotensis</i>	7 (<i>mascotensis</i>)	1.00
<i>ischyrus</i> Goodwin (AMNH 10045)	<i>S. mascotensis</i>	5 (<i>mascotensis</i>)	0.73
<i>borucae</i> Allen (AMNH 171600)	<i>S. hispidus</i>	8 (<i>mascotensis</i>)	0.63
<i>eremicus</i> Mearns (USNM 60319)	<i>S. hispidus</i>	7 (<i>mascotensis</i>)	0.57
<i>tonalensis</i> Bailey (USNM 75144)	<i>S. hispidus</i>	8 (<i>mascotensis</i>)	1.00
<i>saturatus</i> Bailey (USNM 99998)	<i>S. hispidus</i>	5 (<i>mascotensis</i>)	0.70
<i>microdon</i> Bailey (USNM 108467)	<i>S. hispidus</i>	9 (<i>hispidus</i>)	0.92
<i>chiriquensis</i> Allen (AMNH 18789)	<i>S. hispidus</i>	7 (<i>mascotensis</i>)	0.65
<i>griseus</i> Allen (AMNH 28497)	<i>S. hispidus</i>	5 (<i>mascotensis</i>)	0.64
<i>confinus</i> Goldman (USNM 204241)	<i>S. hispidus</i>	5 (<i>mascotensis</i>)	0.69
<i>zanjonensis</i> Goodwin (AMNH 69277)	<i>S. hispidus</i>	7 (<i>mascotensis</i>)	0.98
<i>floridanus</i> Howell (USNM 261624)	<i>S. hispidus</i>	9 (<i>hispidus</i>)	1.00
<i>virginianus</i> Gardner (USNM 273535)	<i>S. hispidus</i>	9 (<i>hispidus</i>)	0.99
<i>komareki</i> Gardner (USNM 207210)	<i>S. hispidus</i>	9 (<i>hispidus</i>)	1.00

pendix). By way of instructive contrast, those holotypes originating from the southeastern U.S.A. (*floridanus*, *komareki*, *virginianus*) did group sensibly with the Floridian sample of *S. hispidus* (Table 6).

Members of the *hispidus* complex, so far as known from the southern U.S.A. to northwestern South America, possess a relatively narrow temporal fossa, tail notably

shorter than head-and-body length, and a diploid number of 52 (Zimmerman & Lee 1968, Kibliskey 1969, Zimmerman 1970), but in pelage color and texture and in cranial form and size, they vary substantially. Based on our review of most relevant types and casual examination of museum series, typical *S. hispidus* appears to comprise those populations in the southeastern

U.S.A. (*floridanus*, *komareki*, *virginianus*), the southern Great Plains (*alfredi*, *texianus*), and the central plateau of northern México (*berlandieri*). To the southwest and south of this moiety, the taxonomic picture becomes muddled. Populations in Arizona—those bearing the names *confinus*, *eremicus*, and *jacksoni*—deserve additional systematic clarification, with respect to their synonymy as *S. hispidus*, as *S. arizonae*, or as something else (Zimmerman 1970, Hoffmeister 1986). Along the Gulf coast of eastern México, across the Isthmus of Tehuantepec, and into the lowlands of the Yucatán Peninsula and northern Guatemala, one finds a group of populations characterized by shorter fur, generally somber brown in color, shorter toothrows, and smaller auditory bullae. The oldest name for these is Saussure's (1860) *toltecus*, which may include the forms *saturatus*, *microdon*, and perhaps *furvus* (Bangs, 1903); Bailey (1902) had mentioned a *toltecus* group within his broad polytypic definition of *S. hispidus*. Hispid cotton rats described from the highlands of Chiapas and western Guatemala, *villae* and *zanjonensis*, respectively, resemble those of the *toltecus* complex in size but possess a longer, more brightly colored pelage; the elevation of the type locality of *zanjonensis*, ca. 2700 m, alone advises caution in accepting the homogeneity of populations now grouped under the epithet in conventional range maps (Hall 1981). The relationships of the Mexican *hispidus*-like forms to populations farther south in Central America—*griseus*, *borucae*, and *chiriquensis*—similarly invite detailed study. As noted by Voss (1992); Burmeister's (1854) *hirsutus*, whose type locality is in northern Venezuela, may assume importance in deciding nomenclatural issues that involve these southernmost populations of the *hispidus* complex.

The number and distribution of species still mistakenly subsumed under "*hispidus*" are topics that require much additional investigation, incorporating other kinds of data and fine-scale geographic sampling.

Like Hooper's (1955) early perceptions of taxonomic differences among *Peromyscus boylii* populations, unraveling the intricate alpha systematic problems that yet surround *Sigmodon* will likely unfold from firm answers attained first on select regional bases.

Taxonomic Summary

Partial synonymies that trace first authorities for new name combinations are given below for *S. arizonae* and *S. mascotensis*. Species-group taxa given under *S. alleni* and *S. hispidus* are intended only as a list of the type specimens we examined, and are not a statement of junior synonyms demonstrated to be conspecific. For the latter, we include names that have been applied only to populations in the southwestern U.S.A., México, and Central America.

Sigmodon arizonae Mearns

Sigmodon hispidus arizonae Mearns, 1890: 287 (type locality—United States, Arizona, Yavapai County, 3 mi SE Camp Verde, Bell's Ranch [as restricted by Hoffmeister 1986]; holotype—AMNH 2370/1841).

Sigmodon arizonae, Zimmerman, 1970:435 (elevation to species).

Sigmodon hispidus major Bailey, 1902:109 (type locality—México, Sinaloa, Sierra de Choix, 50 mi NE Choix; holotype—USNM 96275).—Zimmerman, 1970:446 (synonymy with *S. arizonae*).—Hall, 1981:742 (retention as a subspecies of *S. arizonae*).

Sigmodon hispidus jacksoni Goldman, 1918:22 (type locality—United States, Arizona, Yavapai County, 3 mi N Fort Whipple, near Prescott, 5000 ft; holotype—USNM 214121).—Zimmerman, 1970:446 (synonymy with *S. arizonae*).—Hall, 1981:742 (retention as a subspecies of *S. arizonae*).

Sigmodon hispidus cienegae Howell, 1919: 161 (type locality—United States, Arizona, Pima County, 4 mi E Fort Lowell, Bullock's Ranch; holotype—A. B. How-

ell collection 1531).—Zimmerman, 1970: 446 (synonymy with *S. arizonae*).—Hall, 1981:741 (retention as a subspecies of *S. arizonae*).

Sigmodon hispidus plenus Goldman, 1928: 205 (type locality—United States, Arizona, Yuma County, Parker, 350 ft; holotype—USNM 181086).—Zimmerman, 1970:446 (synonymy with *S. arizonae*).—Hall, 1981:742 (retention as a subspecies of *S. arizonae*).

Distribution.—Extreme southeastern California and southcentral Arizona, U.S.A., southwards along coastal plain and contiguous foothills of the Sierra Madre Occidental in northwestern México, to southcentral Nayarit. In Nayarit, most collecting sites situated in the coastal plain that dominates the northwestern sector of the state, but also at intermediate elevations (1000–1900 m) along the upper drainage of the Río Grande de Santiago (Fig. 18).

Apart from the unresolved status of *jacksoni* (see below), collection records, as reported here and by Hoffmeister (1986), likely delimit the full geographic extent of *S. arizonae*. In our museum searches to redefine the distribution of *S. mascotensis* in western México, we have not encountered examples of *S. arizonae* to the south of the localities now documented from Nayarit. To the northwest—in Sinaloa, Durango, and Sonora—places where the species has been collected lie on coastal plain and lower Pacific-facing slopes of the Sierra Madre Occidental. Along eastern slopes of that mountain axis and onto adjoining plateaus, one finds populations of *S. hispidus* proper, corresponding to the race *S. h. berlandieri* (Baker 1956, Baker & Greer 1962, Anderson 1972, Severinghaus & Hoffmeister 1978, Matson & Baker 1986).

The presence of *S. arizonae* at moderate elevations in eastern Nayarit (Mesa del Nayar, 1300 m; Ocotá Airstrip, 1900 m) appears anomalous in light of the usual occurrence of the species in coastal plain of the westcentral region (Fig. 18). Both kar-

yotypic and morphological data, however, confirm the specific assignment of these outlier populations. Carleton et al. (1982) had noted similar disjunct distributional records among certain Nayarit *Peromyscus* and speculated that riparian vegetation along major rivers, like the Río Grande de Santiago and Río Huayanamota, may provide dispersal corridors to the state's interior. Matson (1982) offered a similar explanation for certain tropical rodent taxa that reach the canyon region of southwestern Zacatecas.

Remarks.—Nayarit samples of this large-bodied *Sigmodon* most closely resemble Bailey's (1902) *S. hispidus major*, described from nearby Sinaloa. Zimmerman's (1970) argument for the taxon's synonymy with Mearn's (1890) *S. arizonae* is persuasive, and our observations and results support his conclusion. While the discriminant scores of the holotypes of *arizonae* and *plenus* fall outside the limits of craniodental variation obtained for the Nayarit series (Fig. 17), a posteriori classification casts the morphological affinity of the Arizonan taxa with them and *major*, not with representatives of *S. hispidus* or *S. mascotensis* (Table 6). Further, some allowance must be duly given for geographic variation, and Zimmerman (1970) had previously remarked that the Sinaloan and Nayarit samples averaged slightly larger than those from Arizona, a distinction reflected in his cluster analysis. Verification of a diploid count of 22 for animals from the type locality of *arizonae*, where specimens have not been collected since 1932 according to Hoffmeister (1986), would help to cement the usage of this name; to date, reported karyotypes represent the taxa *cienegae*, *major*, and *plenus* (Zimmerman 1970, this study).

The invocation of geographic variation less easily explains the unexpected assignment of the type of *S. hispidus jacksoni* to Nayarit *S. mascotensis* (Table 6). Zimmerman (1970) arranged *jacksoni*, also named from Arizona, as another junior synonym of *S. arizonae*, but Hoffmeister (1986) later

Table 7.—Measurements (mm) of type specimens of taxa currently associated with *Sigmodon arizonae*.

	<i>arizonae</i>	<i>major</i>	<i>plenus</i>	<i>jacksoni</i>
Sex	M	M	M	M
Age	A	O	A	J
TOTL	320.0	365.0	316.0	249.0
LT	116.0	156.0	147.0	108.0
LHF	36.0	40.5	36.5	33.0
ONL	40.2	40.4	37.1	31.1
ZB	22.1	23.5	21.7	18.1
IOB	5.5	5.3	5.5	4.9
BBC	14.6	16.0	14.4	14.2
BOC	8.1	8.0	8.2	7.4
DBC	11.7	12.8	12.3	11.1
DTR	4.5	5.7	3.6	3.2
LR	13.6	14.0	12.0	10.0
BR	8.2	8.6	7.4	6.7
PPL	14.0	14.7	13.4	10.0
LBP	7.5	7.5	7.2	6.2
BBP	8.2	8.7	8.5	6.7
LIF	8.6	8.8	8.7	6.3
LD	11.3	11.4	11.1	8.5
BZP	4.4	4.6	4.6	3.3
LZS	4.7	6.2	5.5	4.2
LAB	6.4	6.5	6.6	5.8
LM1-3	6.62	6.96	6.54	6.35
WM1	2.36	2.35	2.22	2.05
DI	2.12	2.53	2.03	1.59
DM	7.4	7.7	7.0	6.1

drew attention to the problematic characteristics of the type, a juvenile and so far the only known specimen. We can only echo Hoffmeister's reservations while assuring that the specimen is not an individual of *S. mascotensis*. It was statistically associated with that species as the best multivariate choice among the taxonomic alternatives offered in our discriminant function analysis and given the weight accorded certain pivotal variables, especially LAB and LM1-3. With regard to both, the molar row and bulla of *jacksoni* are small compared with other holotypes and with the Nayarit series of *S. arizonae* (Table 7, Appendix). Nor does the individual's immature age sufficiently explain the erroneous numerical classification—length of molar row, at least, is age invariant. And we reiterate that inclusion of juveniles in preliminary morphometric comparisons, whether principal

component or discriminant function analyses, did not obscure taxonomic separation among Nayarit species and *S. hispidus*. The conformation of the zygomatic spine in *jacksoni* more closely resembles the condition typical of *S. hispidus* than that of *S. arizonae*. We doubtfully retain Goldman's (1928) *jacksoni* in the synonymy of *S. arizonae* for want of more convincing evidence of its specific relationships and status.

Ecological notes.—Localities where specimens of *S. arizonae* were captured in Nayarit generally fall within the Arid Upper Tropical Subzone (sensu Goldman 1951). The dominant vegetation at these sites was characterized by field personnel as savanna-woodlands, deciduous tropical forest, palm forest, or mangrove swamp. For localities where microhabitat origin can be reasonably determined, however, individual *Sigmodon* were consistently trapped in open grassy and herbaceous settings, usually in the presence of ample water—whether in the form of rivers and their floodplains, lakes and ponds, or drainage sloughs through agricultural fields and pastures. As noted above, *S. arizonae* taken near San Pedro Lagunillas inhabited a dense stand of water hyacinth bordering the small lake, some of the traps placed on floating mats of the plant. At Ocotá Airstrip in southeastern Nayarit (1900 m), surrounded by pine and oak forest, *S. arizonae* were trapped only in grassy patches at the bottom of a nearby arroyo with standing pools of water. Near La Concha, the single specimen of *S. arizonae* was swimming in the shallow Río Canas and caught by hand, after diving straight to the bottom to escape the first attempt at capture.

In view of its presence on coastal plain and along river valleys into Nayarit's interior, *S. arizonae* was collected with a wide variety of rodent species: *Sciurus aureogaster*, *S. colliaei*, *Spermophilus annulatus*, *S. variegatus*, *Pappogeomys bulleri*, *Thomomys umbrinus*, *Chaetodipus pernix*, *Liomys irroratus*, *L. pictus*, *Baiomys tay-*

lori, *Hodomys alleni*, *Neotoma mexicana*, *Oryzomys palustris*, *Peromyscus boylii*, *P. maniculatus*, *P. melanophrys*, *P. pectoralis*, *P. simulus*, *P. spicilegus*, and *Reithrodontomys fulvescens*. It was documented with *S. alleni* in southern coastal plain (Chacala, San Blas) and with *S. mascotensis* in the southern ridge and valley country (2 mi E San Pedro Lagunillas).

Specimens examined.—Durango: Chacala (USNM 96735–96742). Nayarit: Acaponeta (USNM 91398, 91399); near La Concha, Río Canas, Nayarit-Sinaloa state line (USNM 509978); 1 mi S Cuautla (USNM 509980, 510765); Mesa del Nayar, 4500 ft (USNM 511700); Ocotla Airstrip (USNM 523944–523951, 524385); Playa Colorado, 15 km S Santa Cruz (USNM 553988–553995, 554152, 554153); 4 mi E Playa Los Corchos (USNM 553996, 554158); San Blas (USNM 89214); 2 mi E San Pedro Lagunillas, east side of lake (USNM 509999, 510003, 510012, 510013, 510017–510019, 510028–510033, 510035–510037, 510039, 510040, 510042–510045, 510047, 510764, 510765, 510768, 510769, 510771, 510775, 510777, 510780–510783, 510785, 510788, 510791); 6 km S Santa Cruz (USNM 553987, 554151); 1.4 mi N (by rd) Tacote (USNM 509979, 510764); Tepic (USNM 88237). Sinaloa: Ahomé (USNM 131541–131543); Culiacan (USNM 96741); Escuinapa (AMNH 24072–24078, 24080–24084, 24086–24094, 24096–24103, 24105–24117, 24484–24486, 24488, 24490–24492, 24494–24497, 24777, 24778, 24476–24478, 24480–24483, 24889–24891, 25887; FMNH 20098); Microondas La Muralla (USNM 524486, 524487); Pinos Gordo (UMMZ 75265); Plomosas (USNM 91401); Rosario (AMNH 13755; USNM 91400); Sierra de Choix, 50 mi NE Choix (USNM 96270–96275). Sonora: Alamos (USNM 96276–96278); Bacerac (USNM 250901); Nogales (USNM 2213); Magdalena (USNM 17806/24743–17808/24745); 23 km S Nogales (USNM 251032); Oputo (USNM 250902–250903).

Sigmodon mascotensis Allen

Sigmodon mascotensis Allen, 1897b:54 (type locality—México, Jalisco, Mineral San Sebastian, near Mascota, 3300 ft; holotype—AMNH 8321/6655).—Bailey, 1902:108 (reallocated as a subspecies of *S. hispidus*).—Zimmerman, 1970:435 (reinstatement as species).—Hall, 1981:740 (arrangement as nominate subspecies).

Sigmodon colimae Allen, 1897b:55 (type locality—México, Colima, plains of Colima; holotype—AMNH 2648/2318).—Bailey, 1902:108 (synonymy with *S. hispidus mascotensis*).—Allen, 1906:209 (reinstatement as subspecies of *S. hispidus*).—Zimmerman, 1970:446 (synonymy with *S. mascotensis*).—Hall, 1981:741 (full synonymy with *S. m. mascotensis*).

Sigmodon hispidus tonalensis Bailey, 1902:109 (type locality—México, Chiapas, Tonalá; holotype—USNM 75144).

Sigmodon hispidus inexoratus Elliot, 1903:144 (type locality—México, Jalisco, Ocotlan; holotype FMNH 8651).—Hall, 1981:740 (reallocation as a subspecies of *S. mascotensis*).

Sigmodon hispidus [sic] *atratus* Hall, 1949:149 (type locality—México, Michoacan, 6.5 mi W Zamora, 5950 ft; holotype—MVZ 100628).—Russell, 1952:82 (synonymy with *S. hispidus inexoratus* Elliot).—Hall, 1981:740 (full synonymy with *S. mascotensis inexoratus*).

Sigmodon hispidus obvelatus Russell, 1952:81 (type locality—México, Morelos, 5 mi S Alpuyecá, 3700 ft; holotype—TCWC 4921).

Sigmodon hispidus ischyryrus Goodwin, 1956:8 (type locality—México, Oaxaca, Yautepec District, Santo Domingo Chontecomatlán, “El Arco” gorge of Río Grande, 2600 ft; holotype—AMNH 171600).—Zimmerman, 1970:446 (synonymy with *S. mascotensis*).—Hall, 1981:740 (retention as a subspecies of *S. mascotensis*).

Distribution.—Coastal plain, interior basins, and west- and south-facing slopes of western México, from southern Nayarit and southwestern Zacatecas to southern Oaxaca and extreme southwestern Chiapas; occurring at low to intermediate elevations (sea level to 2100 m), most localities of specimens examined falling between 500 and 1500 m; and absent from the highlands of the Transverse Volcanic Range, Sierra Madre del Sur, and northern Oaxaca (Fig. 16). In Nayarit, limited to the southeastern quadrant of the state, mostly in tablelands and low mountains but also collected at low elevation in the valley of the Río Grande de Santiago (Fig. 18).

The range of *S. mascotensis* closely approaches that of the *S. hispidus* complex in three regions where sympatry may be eventually recorded. Two involve relatively arid interior valleys, the Tequisquiapan Valley, in southern Queretaro and western Hidalgo, and the Tehuacán Valley, in western Puebla. The third includes the warm lowlands of the Isthmus of Tehuantepec in western Chiapas and southeastern Oaxaca, where, as perceptively observed by Goodwin (1969:199), "*Sigmodon h. mascotensis* does not intergrade with the smaller short-tailed cotton rats of the *hispidus* group [i.e., *toltecus* and *saturatus*] that are prevalent on the Gulf drainage." The basis of his conviction can be readily grasped when perusing the AMNH series from the Tehuantepec district.

Remarks.—In hindsight, the specific affinity of forms now gathered under synonymy of *S. mascotensis* was predictable from the early descriptions themselves. Thus, Bailey (1902:109) characterized *tonalensis*, his new subspecies of *S. hispidus*, as "Similar to *mascotensis* but larger and slightly browner," and further allowed that "This is merely a large form of *mascotensis*, from which there is no sharp geographic separation." In similar manner, the recurring focus of contrast in the differential diagnosis of the other synonyms has been Allen's (1897b) *S. mascotensis* (Elliot 1903, Hall

1949, Russell 1952, Goodwin 1956), including his own *S. colimae*, which he described in the same publication. With regard to the separation of the latter from *S. mascotensis*, Allen (1897b:55) acknowledged that "I am unable to recognize any distinctive cranial features." Specific recognition, as for many other forms described in the late 1800s, rested upon subtle differences in pelage color or size and those posited from actually few specimens (Allen had available four individuals each of his new species *mascotensis* and *colimae*).

Our examinations of types, referred specimens of original type series, and other museum holdings confirm the morphological homogeneity and probable genetic closeness among those populations now arranged under *S. mascotensis*. Allen's (1897b) type of *S. mascotensis* (AMNH 8321/6655) was consistently associated phenetically with our Nayarit samples (Figs. 2 and 17, Table 6), as were the four other holotypes seen and measured (*colimae*, *tonalensis*, *inexoratus*, and *ischyrus*—Table 6). Pelage color and texture of the latter four, as well as their cranial features, match the general color pattern and morphology of *S. mascotensis*. We did not examine the type of Hall's (1949) *atratus* (MVZ 100628), though Russell's (1952) merger of the Michoacan taxon into full synonymy with *S. hispidus inexoratus*, accepted by Hall & Kelson (1959) and maintained by Hall (1981) as *S. mascotensis inexoratus*, conveys much about the specimen's inseparability from *S. mascotensis*. Hall's own illustration (1949:150, plate IX) of the type specimen strongly suggests an example of *S. mascotensis*, including possession of the oblong paraptertygoid fenestrae; his single referred specimen, from Zamora (USNM 120268), is undoubtedly an example of the species. Nor did we personally study the holotype of Russell's (1952) *obvelatus* (TCWC 4921); however, all other specimens from his original series (TCWC 4920, 4922, 4923) exhibit the characteristic

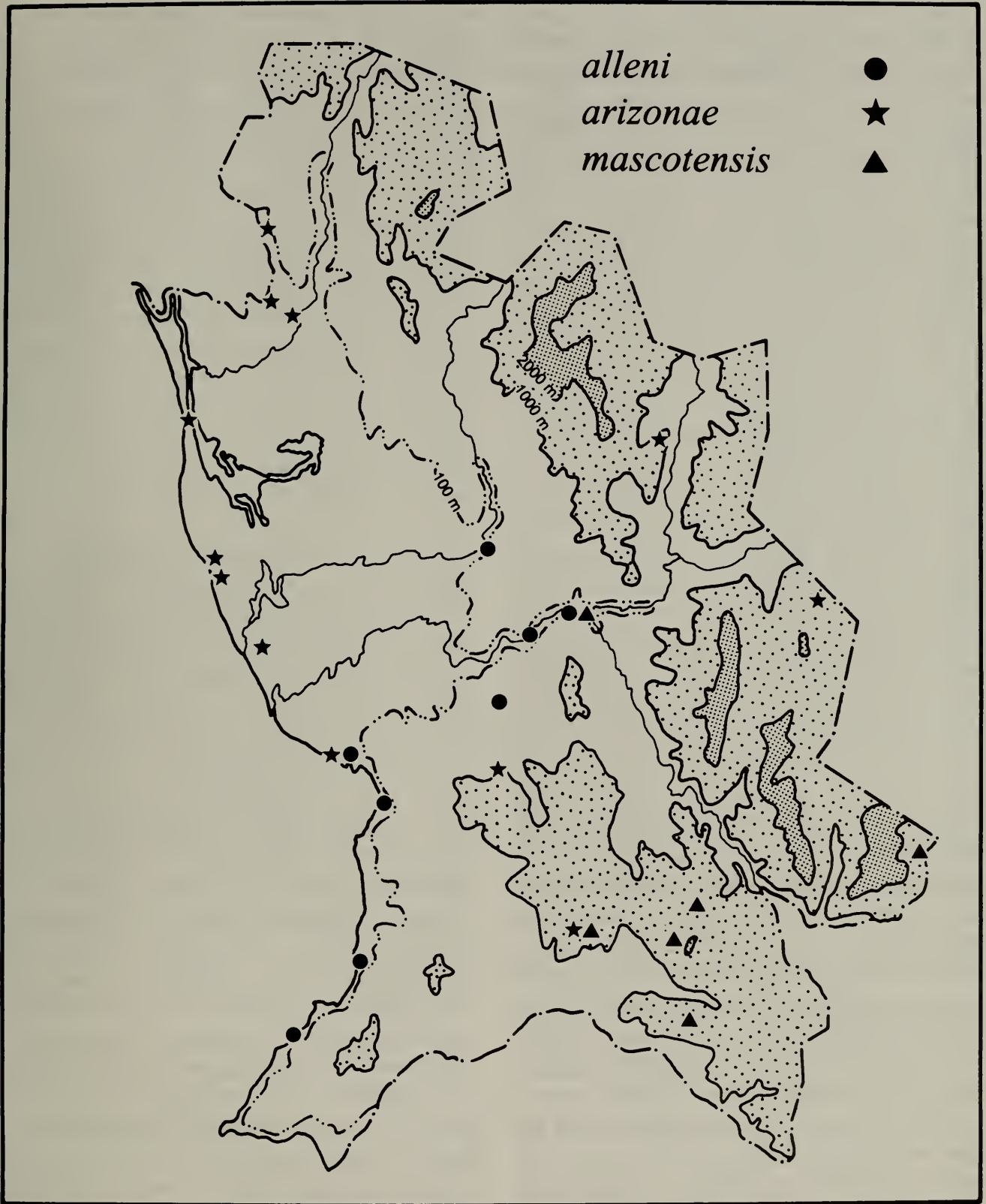


Fig. 18. Distribution of three species of *Sigmodon* in Nayarit, México, based on collections reported herein (dashed-dotted line = 100 m contour; light stipple = elevations between 1000 and 2000 m; dense stipple = elevations above 2000 m).

morphology of *S. mascotensis*, as do others in the USNM collections from Morelos.

In accepting the name changes proposed by Zimmerman (1970), Hall (1981) re-

tained most junior epithets as subspecies of *S. mascotensis*, a nomenclatural formality unsubstantiated by fresh analyses of intra-specific variation. Our qualitative appraisal

Table 8.—Measurements (mm) of type specimens of taxa considered as synonyms of *Sigmodon mascotensis*.

	<i>mascotensis</i>	<i>colimae</i>	<i>tonalensis</i>	<i>inexoratus</i>	<i>ischyrus</i>
Sex	F	M	M	M	M
Age	A	A	O	A	A
TOTL			350.0	310	
LT			166.0	146	145.5
LHF			41.0	36	34.5
ONL	34.7	36.0	38.9	37.1	37.4
ZB	19.5	19.9	22.0	20.5	21.3
IOB	5.2	5.1	5.8	5.0	5.2
BBC	13.5	13.9	14.9	14.3	14.3
BOC	7.4	8.2	8.1	7.7	7.7
DBC	11.5	11.3	12.5	10.9	11.7
DTR	4.2	3.7	4.4	3.9	4.4
LR	12.1	12.0	13.7	12.2	13.4
BR	6.4	6.8	7.8	7.4	7.9
PPL	12.4	12.7	14.0	13.9	14.0
LBP	6.1	6.6	6.3	7.4	6.5
BBP	7.5	8.0	8.3	7.9	8.2
LIF	8.7	7.8	9.7	7.9	8.4
LD	10.0	9.6	11.4	10.7	10.8
BZP	4.0	4.2	4.8	4.4	4.0
LZS	4.7	5.1	5.2	5.8	5.1
LAB	5.4	6.0	5.9	5.6	5.9
LM1-3	6.12	6.61	6.23	6.32	6.13
WM1	2.18	2.20	2.09	2.24	2.10
DI	1.97	2.12	2.21	2.14	2.19
DM	6.2	6.3	7.3	6.7	6.7

of some 500+ museum specimens, collected across the range of *S. mascotensis* as now defined, suggests that such future analyses should devote attention to populations from eastern Oaxaca and contiguous Chiapas. Even allowing for the advanced age of the type specimen of Bailey's (1902) *tonalensis* (Table 8), the populations it represents—for example, those from Tehuantepec and Guiengola, Oaxaca—are impressive for their size, which approximates the dimensions attained by adult *S. arizonae*. In addition, these large Oaxacan animals typically possess a more corrugated palate and pronounced mesopterygoid spine, again more like examples of *S. arizonae* and less like most *S. mascotensis*. Still, in inflation of the bullae, size of the foramen ovale, frequency of parapterygoid fenestrae, and pelage features, these series fit best with *S. mascotensis*.

Apart from the enigmatic combination of

traits found in these southern populations, samples of *S. mascotensis* from the northern and middle parts of its range appear uniform and display the kinds of minor interlocality variation attributable to differences in age composition, molting stage, and collecting season. Further, no chromosomal variation is thus far known for populations distributed over this region, from Nayarit to western Oaxaca (Zimmerman 1970, this report). To our knowledge, chromosomes of named forms from eastern Oaxaca (*ischyrus*) or western Chiapas (*tonalensis*) have yet to be examined.

Ecological notes.—*Sigmodon mascotensis* was common in the southern part of Nayarit, where most collecting sites represent the Arid Lower Tropical Subzone (Goldman 1951). The region is topographically diverse with low mountains and tablelands dissected by river valleys and steeply eroded arroyos. Ridges are covered

with tropical deciduous forest that grades into oak and pine-oak woodland associations at the upper elevations; meandering streams and valley bottoms, rocky outcrops and old lava flows afford ample terrain for open grass and brush stands and mixed savanna-scrublands. Where verifiable, specimens of *S. mascotensis* originated from the latter habitats, as well as from around agricultural fields bordered with rank brush. At Estanzuela, traplines that produced *S. mascotensis* ran through grassland and broken pine-oak woods and along a stream-bank covered with ferns. South of Ahuacatlan, examples of *S. mascotensis* were captured in tall grasses interspersed among rocks, bare soil, and scattered oaks and cactus.

In addition to *Sigmodon alleni* and *S. arizonae*, *S. mascotensis* was documented sympatrically with *Sciurus aureogaster*, *S. colliaei*, *Spermophilus variegatus*, *Pappogeomys bulleri*, *Liomys irroratus*, *L. pictus*, *Baiomys taylori*, *Neotoma mexicana*, *Oryzomys melanotis*, *O. palustris*, *Peromyscus maniculatus*, *P. melanophrys*, *P. pectoralis*, *P. spicilegus*, and *Reithrodontomys fulvescens*. The locality of sympatry with *S. alleni*, Arroyo de Jiguite near its confluence with the Río Grande de Santiago (100 m), is situated in a lowland region where a number of intermediate- to high-elevation *Peromyscus* species were unexpectedly found to occur (Carleton et al. 1982).

Specimens examined.—Chiapas: Cintalapa, Cinco Cerros (AMNH 148825–148828); Cintalapa, 555 m (UMMZ 92476, 94033–94035, 96306); Tonalá (AMNH 167430, 167431); mountains near Tonalá (USNM 75144, 76089). Colima: Armería, sea level–200 ft (USNM 33323/45351–33332/45360, 34185); Colima, 1700 ft (USNM 33333/45361–33341/45369); plains of Colima (AMNH 2646/2319, 2647/2129, 2648/2318, 2649); 3 mi SE Colima (UMMZ 100693, 100694). Guerrero: 0.5 mi W Acahuizotla, 3000 ft (UMMZ 109205); Acapulco, near sea level (USNM 70764); Agua del Obispo, 2900 ft (UMMZ

108558); Chilpancingo, 4800 ft (FMNH 47550, 47552, 47554–47557, 48466, 51947–51949; UMMZ 81461–81470, 84015, 84016, 89262, 104977–104991; USNM 70300, 70760–70763); Cuapongo (FMNH 47553); El Limón (126530, 126531); Iguala, 750 m (UMMZ 92597, 93455–93462); near Ometepe, 200 ft (USNM 71575, 71576); Tlalixtaquilla, 4200 ft (USNM 70234). Jalisco: Ameca, 4000 ft (USNM 82247); 6 mi W Ameca, 4300 ft (UMMZ 95495–95499); 7 mi W Ameca, 4000 ft (UMMZ 95500); Atenguique (AMNH 26322–26324); Atemajac, 4500 ft (USNM 34146/46223); 4 mi NE Autlán, 3000 ft (UMMZ 95501–95507, 96268); Estancia (AMNH 25289, 25346, 25350, 25357, 25358, 25364–25366); Huejuquilla, 5400 ft (USNM 90810); Lagos, 6150 ft (USNM 78969, 80348); Las Canoas (AMNH 26317–26321, 26551–26557); Mascota, Mineral San Sebastián, 3300 ft (AMNH 8321/6655, 8322/6656); 0.5 mi W Mazamitla (UMMZ 100695, 100696, 100698); Ocotlán, 5000 ft (FMNH 8651–8653, 8656–8658, 8660–8662, 8664–8666; USNM 120153–120159); Ojo de Agua, near Amatlán (AMNH 25360); Rancho Palo Amarillo, near Amatlán (AMNH 25353–25356); Arroyo de Plantanar (AMNH 25348, 25349, 25361); 2 mi N Resolana, 1500 ft (UMMZ 95510–95512); Río Santa María (AMNH 25347, 25359); Tuxpan (AMNH 26293, 26294); Zacoalco, 3000 ft (USNM 34143/46220–34145/46222); Zapotlán, 4000 ft (USNM 3359/45624, 33590/45625). Michoacan: Hacienda El Molino (USNM 20440/35670); La Huacana (USNM 126522–126529); La Salada (USNM 126520, 126521); 9.6 mi S Lombardía, 1400 ft (UMMZ 110562, 110563); Los Reyes (USNM 125933–125935); Queréndaro, 5800 ft (USNM 50201); 12 mi S Tzitzio, road to Huetamo, 1050 m (UMMZ 92214); Zamora (USNM 120268). Morelos: 5 mi S Alpuyeca, 3500 ft (TCWC 4921, 4922); Cuernavaca, 5000 ft (USNM 51164, 51165); 2 km S Jonacatepec, 4500 ft (TCWC 4920); Puente de

Ixtla (USNM 126938–126940); Yautepec, 4100 ft (USNM 51166–51169); 6 mi W Yautepec, 6000 ft (TCWC 4923). Nayarit: 8 mi S (by rd) Ahuacatlán (USNM 523952–523955); Amatlán (AMNH 25345, 25351, 25352); Arroyo de Jiguite, Río Santiago, 100 m (USNM 523956–523977, 523979–523981, 523983–523986, 524386–524392); 1.8 mi NW (by rd) Coapan, 4650 ft (USNM 511701); Estanzuela (USNM 510051–510058, 510793–510799); Rancho Sapotito, 3500 ft (USNM 511702–511706, 511756); 1 mi SW San José del Conde, 3000 ft (UMMZ 95492–95494); 2 mi E San Pedro Lagunillas, east side of lake (USNM 509982–509998, 510000–510002, 510004–510011, 510014–510016, 510020–510027, 510034, 510038, 510041, 510046, 510048–510050, 510766, 510767, 510770, 510772–510774, 510776, 510778, 510779, 510784, 510786, 510787, 510789, 510790, 510792); 2 mi N Santa Isabel, 3800 ft (UMMZ 95490, 95491). Oaxaca: Agua Blanca, 4000 ft (AMNH 145823); Buena Vista (AMNH 145252); Cerro Calderona, 3000 ft (AMNH 147696); Cuicatlán, 640 m (UMMZ 96801); Escuranos (AMNH 143950); Guiengola, 3600 ft (AMNH 142522, 142523, 142530–142533, 143432, 143951, 147697–147712); Huajuapam, 5500 ft (USNM 70233, 70235, 70236); Huilotepec (AMNH 143430); Jalapa (AMNH 171618, 171619, 175188–175191); Juchitán (AMNH 175193–175197); La Reforma (AMNH 175192; FMNH 14100, 14102); 5 km N Las Cuevas (AMNH 142524–142527); Limón (AMNH 186920); Miahuatlán (UMMZ 94032); Mixtequilla (AMNH 175186); Morro Mazatlán (AMNH 167432, 171607, 171654); Nizanda (AMNH 175253); Oaxaca, 5000 ft (USNM 68230, 68652–68654); Cerro Palma de Oro (AMNH 147717); Cerro Pozo Río (AMNH 142529, 148816, 148817); Puerto Angel, 100–300 ft (USNM 71577–71581); Reforma, 50 m and 100 m (UMMZ 96805, 96806); Rincón Bamba (AMNH 148819–148823); Sacatepec (AMNH 189288); San Antonio (AMNH 143425–143427, 143477); San

Dionisio, Buena Vista (AMNH 145992–145997); San Pedro Jilotepec (AMNH 145249, 149922, 149923); Santa Lucía (AMNH 144572); Santiago Lachiguiri (AMNH 145832–145835); Santo Domingo, 900 ft (AMNH 3096/2415; USNM 73316–73318); Cerro Sombrerito (AMNH 145831); Tamazulapam, 7000 ft (USNM 70231, 70232); Tapanatepec (AMNH 177093–177100, 177980); Tehuantepec, 150 ft (AMNH 142535, 147713, 147714, 148824, 171608–171617, 171620, 171621, 171655–171658, 175184, 175185, 175187; USNM 9672/9508, 9673/9509, 9671/9510, 11907, 13071, 13072, 73315); 50 mi N Tehuantepec (AMNH 174811); Teotitlán, 950 m (UMMZ 89263, 89264, 91602); Tequisistlán (AMNH 143420–143424); Cerro de Tigre (AMNH 142534, 147716); Zanatepec (FMNH 14101). Puebla: Tehuacán (UMMZ 89250–89260, 89323; USNM 9385/8667); 2 mi W Tehuacán, 5200 ft (UMMZ 103188); Tepanco (UMMZ 89261). Queretaro: Cadereyta, 2100 m (UMMZ 93737); Tequisquiapam (USNM 78427). Zacatecas: 6 km S Apozol, 1170 m (MSU 27240); 16 km SSE Monte Escobedo, 2010 m (MSU 27241–27247); 5 km NE San Juan Capistrano, near Las Tablas, 1330 m (MSU 23645); 18 km N San Juan Capistrano, near Las Tablas, 1100 m (MSU 27234–27239); 2 mi N Santa Rosa, 3850 ft (MSU 11668, 12475); Valparaíso, 6200 ft and 6500 ft (USNM 92008–92010).

Sigmodon alleni Bailey

Sigmodon alleni Bailey, 1902:112 (type locality—México, Jalisco, San Sebastian, Mascota; holotype—USNM 88227).

Sigmodon vulcani Allen, 1906:247 (type locality—México, Jalisco, Volcán de Fuego, 3050 m; holotype—AMNH 26310).

Sigmodon guerrerensis Nelson & Goldman, 1933:196 (type locality—México, Guerrero, Omilteme, 8000 ft; holotype—USNM 126936).

Sigmodon planifrons Nelson & Goldman, 1933:197 (type locality—México, Oaxa-

ca, Juquila, 5000 ft; holotype—USNM 71918).

Sigmodon planifrons minor Goodwin, 1955:1 (type locality—México, Oaxaca, District of Tehuantepec, 12 km NE Tenango, Santa Lucía, 4000 ft; holotype—AMNH 143429).

Sigmodon macdougalli Goodwin, 1955:3 (type locality—México, Oaxaca, 12 km S Yautepec, Santo Tomás Teipán, 7000 ft; holotype—AMNH 149122).

Sigmodon macrodon Goodwin, 1955:4 (type locality—México, Oaxaca, District of Tehuantepec, 20 km W Mixtequilla, Cerro San Pedro; 3600 ft; holotype—AMNH 142536).

Sigmodon planifrons setzeri Goodwin, 1959:447 (replacement name for *S. planifrons minor* Goodwin, 1955, preoccupied by *S. minor* Gidley, 1922).

Distribution.—Pacific coastal lowlands and contiguous slopes of western cordilleras, from southern Sinaloa to central Oaxaca (see Baker 1969, Shump & Baker 1978). In Nayarit, at low elevations (sea level to 760 m) in the southwestern quadrant of the state, the deepest interior records found along the lower valleys of the Río San Pedro and the Río Grande de Santiago (Fig. 18).

The geographic range of *S. alleni*, as presently understood, is partly congruent with the revised distribution of *S. mascotensis*. Individuals of the former, however, apparently prefer more mesic habitats, which may explain the species' occurrence farther north into Sinaloa and at higher elevations, up to 3050 m and into pine-oak vegetation (Baker 1969), as well as its absence from the upper drainage of the Río Balsas and Lago de Chapala, dryer interior basins where *S. mascotensis* is found. Nevertheless, the geographic range of *S. alleni* deserves further documentation, as we have encountered many instances of specimens mistakenly intermixed with *S. mascotensis* in museum collections.

Remarks.—In his description of *S. alleni*,

Bailey (1902) recorded the co-occurrence of his new species with *mascotensis* at San Sebastián, Jalisco, and with *major* (now = *S. arizonae*) at San Blas, Nayarit. Based on these records of overlap, Bailey diagnosed *alleni* as a species and relegated all other members of his *hispidus* group to subspecies of the latter. While explaining his choice of patronym, he continued (1902: 113), "It [*S. alleni*] is the species Dr. Allen had in mind in writing his description of *mascotensis* from which he intended to separate the Colima form, but as the two specimens of the species here named *alleni* were not fully adult he unfortunately selected as his type another specimen that proves to be the same as the form to which on the following page he gave the name *colimae*." Allen (1906) continued to recognize *colimae* as distinct from *mascotensis*, but we concur with Bailey's taxonomic judgement regarding both the synonymy of *colimae* under *mascotensis* and their specific distinction from *S. alleni*. The possibility of confusion is understandable, as we noted above under the morphometric results, particularly when separating isolated skulls of *S. alleni* from those of *S. mascotensis*.

The junior synonyms that have accrued to Bailey's *S. alleni*, following Baker (1969) and Shump & Baker (1978), require substantiation. To us, their arrangement as a single species seems improbable. Although they exhibit the reddish brown dorsum and softer fur typical of *alleni* sensu lato, the types of *planifrons* and *planifrons setzeri* are strikingly diminutive in all dimensions of the skin and skull—particularly as reflected in the narrow incisors, delicate molar rows, constricted interorbit, tiny otic capsules, and shorter tail—compared with *alleni*-like taxa also described from Oaxaca (*macdougalli* and *macrodon*) or with typical *alleni* from farther north (including *vulcani* and *guerrerensis*). The divergent treatment of *planifrons* by Goodwin (1969), who retained it as a species, and Baker (1969), who relegated it to a subspecies of *S. alleni* (along with *macdougalli*

and *macrodon* in full synonymy) warrants reconciliation. It is noteworthy that Goodwin (1969) had identified both *planifrons* and *macdougalli* from Santa Lucia, Oaxaca, the type locality of his (1955, 1959) *planifrons setzeri*. Renewed study of the Oaxacan forms will prove critical to much-needed revision of the *S. alleni* complex.

Ecological notes.—Other rodents captured at localities with *Sigmodon alleni* include *Sciurus colliaei*, *Spermophilus annulatus*, *Thomomys umbrinus*, *Liomys pictus*, *Baiomys taylori*, *Hodomys alleni*, *Neotoma mexicana*, *Oryzomys melanotis*, *O. palustris*, *Osgoodomys banderanus*, *Peromyscus maniculatus*, *P. melanophrys*, *P. pectoralis*, *P. simulus*, and *P. spicilegus*. Records of sympatry with other *Sigmodon* appear to fall where coastal plain meets southern foothills, with *S. arizonae* at San Blas and with *S. mascotensis* at Arroyo de Jiguite.

Specimens examined.—Nayarit: Arroyo de Jiguite, Río Santiago, 100 m (USNM 523935, 523978, 523982, 523987, 523988); 4 km S Aticama (USNM 524479, 524480); Chacala (USNM 523934); 1.2 mi S (by rd) El Casco, Río Chilte, 480 ft (USNM 511697–511699); 3.5 mi E (by rd) El Venado (USNM 509981); 1 km S La Villita (524478); 1 mi S Lo de Marcos, sea level (USNM 523936–523943); San Blas (USNM 89212, 89213); 3.5 mi E San Blas, 100 ft (UMMZ 100680, 100681).

Sigmodon hispidus

Sigmodon berlandieri Baird, 1855:333 (type locality—México, Coahuila, Río Nasas; holotype—USNM 566/1687).

Sigmodon borucae Allen, 1897a:40 (type locality—Costa Rica, Puntarenas, Boruca; holotype—AMNH 11761/10045).

Sigmodon hispidus eremicus Mearns, 1897:4 (type locality—México, Sonora, Cienega Well, 30 mi S monument no. 204, Mexican boundary line; holotype—USNM 60319).

Sigmodon hispidus saturatus Bailey, 1902:

111 (type locality—México, Tabasco, Teapa; holotype—USNM 99998).

Sigmodon hispidus microdon Bailey, 1902:111 (type locality—México, Yucatán, Puerto Morelos; holotype—USNM 108467).

Sigmodon borucae chiriquensis Allen, 1904:68 (type locality—Panamá, Chiriquí, Boqueron; holotype—AMNH 18789).

Sigmodon hispidus griseus Allen, 1908:657 (type locality—Nicaragua, Chontales, coastal lowlands; holotype—AMNH 28497).

Sigmodon hispidus confinis Goldman, 1918:21 (type locality—United States, Arizona, Graham County, Safford, 2900 ft; holotype—USNM 204241).

Sigmodon zanjonensis Goodwin, 1932:1 (type locality—Guatemala, Zanjon, 9000 ft; holotype—AMNH 69277).

Sigmodon hispidus villae Goodwin, 1958:2 (type locality—México, Chiapas, 5 mi E Teopisca, 6000 ft; holotype—AMNH 174799).

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Appendix.—Descriptive statistics for selected cranial and external variables and OTUs of *Sigmodon*.

Species	OTU	<i>n</i>	Mean	Range	<i>SD</i>
Total length					
<i>S. alleni</i>	OTU 1	14	245.8	221.0–278.0	16.3
<i>S. arizonae</i>	OTU 3	15	305.5	247.0–363.0	33.6
<i>S. mascotensis</i>	OTU 5	20	278.1	242.0–313.0	20.1
	OTU 6	32	257.0	220.0–305.0	21.4
<i>S. hispidus</i>	OTU 9	44	250.8	220.0–282.0	18.4
Tail length					
<i>S. alleni</i>	OTU 1	14	110.2	91.0–130.0	10.7
<i>S. arizonae</i>	OTU 3	15	124.4	101.0–145.0	13.6
<i>S. mascotensis</i>	OTU 5	20	132.3	110.0–156.0	12.3
	OTU 6	32	112.3	96.0–141.0	10.5
<i>S. hispidus</i>	OTU 9	44	99.1	81.0–115.0	8.6
Hindfoot length					
<i>S. alleni</i>	OTU 1	17	30.2	27.0–32.0	1.4
<i>S. arizonae</i>	OTU 3	19	38.5	34.0–43.0	2.3
<i>S. mascotensis</i>	OTU 5	21	34.1	31.0–38.0	1.9
	OTU 6	33	35.0	31.0–38.0	1.7
<i>S. hispidus</i>	OTU 9	47	33.3	31.0–36.0	1.3
Mass (Weight)					
<i>S. alleni</i>	OTU 1	17	72.1	49.0–106.0	15.9
<i>S. arizonae</i>	OTU 3	19	150.3	83.0–300.0	54.8
<i>S. mascotensis</i>	OTU 5	21	99.6	63.0–148.0	22.6
	OTU 6	33	77.4	51.0–122.0	17.8
<i>S. hispidus</i>	OTU 9	15	89.8	68.0–144.0	18.3
Occipitonasal length					
<i>S. alleni</i>	OTU 1	17	32.1	27.9–36.0	2.2
<i>S. arizonae</i>	OTU 3	21	35.2	27.4–40.4	3.5
<i>S. mascotensis</i>	OTU 5	27	32.8	29.8–37.0	1.9
	OTU 6	40	31.6	27.5–35.3	1.7
<i>S. hispidus</i>	OTU 9	50	34.6	30.2–37.7	1.8
Zygomatic breadth					
<i>S. alleni</i>	OTU 1	20	17.8	15.8–19.8	1.0
<i>S. arizonae</i>	OTU 3	25	20.9	17.4–23.8	1.6
<i>S. mascotensis</i>	OTU 5	27	18.7	17.0–20.7	1.0
	OTU 6	45	18.3	15.6–20.7	1.0
<i>S. hispidus</i>	OTU 9	53	19.3	16.3–21.1	1.0
Interorbital breadth					
<i>S. alleni</i>	OTU 1	19	5.0	4.6–5.6	0.1
<i>S. arizonae</i>	OTU 3	25	5.1	4.5–5.6	0.3
<i>S. mascotensis</i>	OTU 5	27	4.9	4.5–5.5	0.3
	OTU 6	45	5.0	4.6–5.4	0.2
<i>S. hispidus</i>	OTU 9	53	5.1	4.4–5.7	0.2
Breadth of braincase					
<i>S. alleni</i>	OTU 1	19	13.7	12.9–14.3	0.4
<i>S. arizonae</i>	OTU 3	21	14.9	13.9–16.3	0.6
<i>S. mascotensis</i>	OTU 5	27	14.0	13.1–14.7	0.4
	OTU 6	43	13.9	12.6–14.6	0.4
<i>S. hispidus</i>	OTU 9	53	14.4	13.3–15.4	0.5

Appendix.—Continued.

Species	OTU	<i>n</i>	Mean	Range	<i>SD</i>
Breadth of occipital condyles					
<i>S. alleni</i>	OTU 1	20	7.3	6.7–7.8	0.3
<i>S. arizonae</i>	OTU 3	20	8.1	6.9–8.8	0.5
<i>S. mascotensis</i>	OTU 5	27	7.4	6.9–8.0	0.3
	OTU 6	41	7.5	6.9–8.2	0.3
<i>S. hispidus</i>	OTU 9	52	7.5	6.1–8.0	0.3
Depth of braincase					
<i>S. alleni</i>	OTU 1	19	10.2	9.3–11.3	0.5
<i>S. arizonae</i>	OTU 3	19	11.7	9.9–12.9	0.9
<i>S. mascotensis</i>	OTU 5	27	11.3	10.8–12.2	0.3
	OTU 6	41	10.8	8.9–11.7	0.5
<i>S. hispidus</i>	OTU 9	52	10.7	9.8–11.6	0.4
Distance between temporal ridges					
<i>S. alleni</i>	OTU 1	20	3.3	2.7–3.9	0.3
<i>S. arizonae</i>	OTU 3	24	4.4	3.3–5.0	0.4
<i>S. mascotensis</i>	OTU 5	27	4.0	3.3–4.8	0.4
	OTU 6	45	3.7	2.5–4.4	0.4
<i>S. hispidus</i>	OTU 9	53	3.2	2.5–4.1	0.3
Length of rostrum					
<i>S. alleni</i>	OTU 1	17	10.7	9.1–12.5	1.0
<i>S. arizonae</i>	OTU 3	25	11.6	8.3–13.7	1.3
<i>S. mascotensis</i>	OTU 5	27	10.6	9.0–12.7	0.9
	OTU 6	43	10.3	8.1–11.7	0.7
<i>S. hispidus</i>	OTU 9	50	11.6	9.8–13.0	0.8
Breadth of rostrum					
<i>S. alleni</i>	OTU 1	20	6.5	5.5–7.5	0.5
<i>S. arizonae</i>	OTU 3	24	7.0	5.4–8.9	0.8
<i>S. mascotensis</i>	OTU 5	27	6.4	5.5–7.4	0.5
	OTU 6	45	6.3	5.3–7.2	0.4
<i>S. hispidus</i>	OTU 9	53	6.7	5.7–7.8	0.5
Postpalatal length					
<i>S. alleni</i>	OTU 1	19	11.2	9.3–12.8	0.9
<i>S. arizonae</i>	OTU 3	20	12.8	9.6–15.5	1.6
<i>S. mascotensis</i>	OTU 5	27	11.5	10.0–13.2	0.8
	OTU 6	41	10.9	9.2–12.7	0.7
<i>S. hispidus</i>	OTU 9	52	12.1	5.6–7.3	0.4
Length of bony palate					
<i>S. alleni</i>	OTU 1	20	6.1	5.4–7.1	0.5
<i>S. arizonae</i>	OTU 3	25	6.6	5.3–8.0	0.5
<i>S. mascotensis</i>	OTU 5	27	6.1	5.2–6.9	0.4
	OTU 6	45	6.1	5.1–6.8	0.4
<i>S. hispidus</i>	OTU 9	53	6.6	5.6–7.3	0.4
Breadth of bony palate					
<i>S. alleni</i>	OTU 1	20	7.2	6.7–8.1	0.4
<i>S. arizonae</i>	OTU 3	25	8.1	6.7–9.2	0.5
<i>S. mascotensis</i>	OTU 5	27	7.2	6.7–8.0	0.4
	OTU 6	45	7.4	6.8–8.0	0.3
<i>S. hispidus</i>	OTU 9	53	7.7	6.7–8.5	0.3

Appendix.—Continued.

Species	OTU	<i>n</i>	Mean	Range	<i>SD</i>
Length of incisive foramen					
<i>S. alleni</i>	OTU 1	20	6.7	5.8–7.6	0.5
<i>S. arizonae</i>	OTU 3	25	8.0	6.2–9.7	0.9
<i>S. mascotensis</i>	OTU 5	27	6.9	5.9–8.2	0.6
	OTU 6	45	6.7	5.5–7.8	0.5
<i>S. hispidus</i>	OTU 9	53	7.8	6.2–9.0	0.6
Length of diastema					
<i>S. alleni</i>	OTU 1	20	8.6	7.2–10.2	0.8
<i>S. arizonae</i>	OTU 3	25	9.8	7.3–12.1	1.3
<i>S. mascotensis</i>	OTU 5	27	8.7	7.6–10.3	0.7
	OTU 6	45	8.3	6.3–9.7	0.7
<i>S. hispidus</i>	OTU 9	53	9.5	7.7–11.2	0.8
Breadth of zygomatic plate					
<i>S. alleni</i>	OTU 1	20	3.6	3.0–4.1	0.3
<i>S. arizonae</i>	OTU 3	25	4.1	3.1–5.1	0.5
<i>S. mascotensis</i>	OTU 5	27	3.6	2.8–4.5	0.4
	OTU 6	45	3.7	3.0–4.6	0.3
<i>S. hispidus</i>	OTU 9	53	3.9	2.6–4.8	0.4
Length of zygomatic spine					
<i>S. alleni</i>	OTU 1	20	3.8	3.1–4.4	0.4
<i>S. arizonae</i>	OTU 3	25	5.0	3.6–5.9	0.7
<i>S. mascotensis</i>	OTU 5	27	4.3	3.3–4.9	0.4
	OTU 6	46	4.4	3.2–5.5	0.5
<i>S. hispidus</i>	OTU 9	53	4.5	3.2–5.5	0.5
Length of auditory bulla					
<i>S. alleni</i>	OTU 1	20	5.1	4.6–5.6	0.3
<i>S. arizonae</i>	OTU 3	24	6.1	5.3–6.8	0.3
<i>S. mascotensis</i>	OTU 5	27	5.3	4.9–5.8	0.2
	OTU 6	43	5.3	4.7–5.8	0.2
<i>S. hispidus</i>	OTU 9	53	6.3	5.7–7.0	0.3
Length of maxillary toothrow					
<i>S. alleni</i>	OTU 1	20	5.70	5.36–6.13	0.19
<i>S. arizonae</i>	OTU 3	25	6.82	6.30–7.39	0.25
<i>S. mascotensis</i>	OTU 5	27	5.95	5.59–6.78	0.26
	OTU 6	46	6.23	5.80–6.63	0.23
<i>S. hispidus</i>	OTU 9	53	6.39	6.00–6.81	0.18
Width of upper first molar					
<i>S. alleni</i>	OTU 1	20	1.90	1.76–2.03	0.08
<i>S. arizonae</i>	OTU 3	25	2.29	2.12–2.47	0.09
<i>S. mascotensis</i>	OTU 5	27	2.01	1.84–2.26	0.09
	OTU 6	46	2.09	1.94–2.34	0.08
<i>S. hispidus</i>	OTU 9	53	2.15	1.91–2.32	0.08
Depth of upper incisor					
<i>S. alleni</i>	OTU 1	20	1.81	1.47–2.12	0.09
<i>S. arizonae</i>	OTU 3	25	2.01	1.53–2.37	0.22
<i>S. mascotensis</i>	OTU 5	27	1.81	1.52–2.07	0.08
	OTU 6	46	1.85	1.47–2.17	0.15
<i>S. hispidus</i>	OTU 9	53	1.99	1.52–2.22	0.16
Depth of mandible					
<i>S. alleni</i>	OTU 1	20	5.8	5.1–6.6	0.4
<i>S. arizonae</i>	OTU 3	25	6.6	5.2–7.6	0.6
<i>S. mascotensis</i>	OTU 5	27	5.9	5.3–6.7	0.4
	OTU 6	46	5.8	4.7–6.7	0.4
<i>S. hispidus</i>	OTU 9	53	6.4	5.4–7.2	0.4